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WHITE-TAILED DEER ALONG THE LOWER YELLOWSTONE

BY GARY L. DUSEK

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FINAL REPORT

RESEARCH PROJECT

STATE: Montana

PROJECT NO.: W-120-R-12-18 TITLE: Statwide Wildlife Research

PROGRAM NO.: I TITLE: Big Game Research

STUDY NO.: BG-2.0 TITLE: Statewide White-tailed Deer Ecology Studies

JOB NO.: 3 TITLE: Population ecology and habitat relationships of white-tailed deer in river bottom habitat in eastern Montana

Period Covered: July 1, 1980 - June 30, 1987

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Date: March 31, 1988

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ACKNOWLEDGEMENTS

We extend our gratitude to numerous employees of the Montana Department of Fish, Wildlife and Parks, students at Montana State University, and others for their assistance in data collection. We thank K. L. Hamlin, D. F. Pac, and A. K. Wood for their assistance with data collection and analysis and editorial reviews of the manuscript. The editorial comments provided by C. D. Eustace and weather severity indexes calculated by H. E. Jorgensen are also appreciated. Administrative support and assistance were provided by K. G. Seaburg and J. P. Weigand. We also extend our appreciation to the Ft. Keogh Livestock and Range Research Station, Miles City, MT, and the Department of Animal Science, University of Idaho, Moscow, for analysis of blood sera. Individual contributions of R. B. Campbell, M. Friedman, R. W. Hay, K. A. Kinden, R. B. Staigmiller, R. P. Stoneberg, and K. C. Walcheck, are gratefully acknowledged. We thank all private landowners for granting access to their lands and cooperation.

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ABSTRACT

Population characteristics and habitat relationships of white-tailed deer (Odocoileus virginianus dakotensis) were studied on bottomlands of the lower Yellowstone River in eastern Montana during 1980-86. Early autumn populations on the 224 km^2 study area varied between 3,100 and 5,784 deer. Total numbers increased during 1980-83 and declined during 1984-86 in response to density influenced fawn recruitment and hunter harvests. The population was characterized by relatively high productivity and a predominantly young age structure. The average fawn:doe ratio for autumn was 85:100 (64-112:100). Fawns comprised 32-43% of autumn populations, while deer 2 years and younger accounted for 63% of all females and 93% of all males. Only 5% of the female segment was 8 years and older. Antlered males made up 16-23% of pre-hunt populations; less than 1% were 4 years and older.

Fetal measurements indicated a median breeding date of 21 November. The incidence of successful breeding among female fawns was low (< 2%); the pregnancy rate for older females was 93%. Ovulation rates were 1.41 for yearlings and 2.09 for older females; fetal rates were 1.26 and 1.88, respectively. Age-specific reproduction and recruitment rates increased through age classes 5-6 (6-7 years at parturition) and declined among older females. Reproductive success varied inversely with density of adult females; females in age classes 2 and 3 were most affected. Average annual mortality rates were 50% for fawns, 22% for adult females, and 60% for adult males. Neonatal and summer mortality accounted for 32% of all fawns produced and varied directly with adult female density. Hunting accounted for 81% of all mortality documented among deer older than 6 months and 13-35% of autumn populations. Hunting-related mortality equalled or exceeded fawn recruitment during 1983-86, years of population decline. Intense hunter selection of antlered over antlerless deer contributed to a skewed sex ratio among adults favoring females (~2:1) in early autumn. Average mortality rates were low in winter among fawns (10%) and adults (6%) and were not significantly correlated with winter severity. Low overwinter mortality, high productivity, and seasonal trends in whole weights and kidney fat indexes (KFI) collectively indicated that the population wintered on a high nutritional plane.

The relative abundance of woody cover accounted for 74% of the variation in density distribution of deer along the river bottom. The amount of island area, sloughs, and livestock distribution also influenced distribution of deer. Deer were generally nonmigratory, occupying relatively small home ranges that overlapped seasonally within the river bottom. Diurnal home ranges were typically smaller during summer than winter. Diel home ranges were twice as large as diurnal home ranges during summer and 3 times larger in winter. Females exhibited a higher fidelity to summer than winter home ranges. Diurnal movement indexes among adult deer were typically lowest during June-August and highest during November. The most distinct daily movements were from riparian cover used during daytime to agricultural

fields at night. Nocturnally, deer generally selected alfalfa fields during summer and sugar beet or cereal grain fields during winter; however, seasonal selection for specific crop types and riparian forest/shrub communities varied temporally and spatially with availability and sex and age of deer. Adult females used habitats having greater diversity of cover types, including agricultural fields and forest types with a shrub/herbaceous understory, than those used by adult males. Agricultural crops accounted for 41% of the yearlong diet; spatially, increased use of crops or crop residues coincided with decreased use of browse.

The current widespread distribution and high relative abundance of white-tailed deer along the lower Yellowstone River appeared to reflect habitat changes brought about by settlement, elimination or reduction of other wild ungulates, and land use practices. An intensively farmed river bottom with a relatively undisturbed riparian forest/shrub complex provided a highly diverse, stable and predictable habitat-environmental complex within a highly variable and unpredictable regional environment. Observed patterns of habitat useage, that included dispersed distribution and limited movement within high quality cover-forage complexes during late spring and summer, were consistent with optimal opportunity to sustain high female densities and successfully rear fawns. Population characteristics and dynamics were not consistent with traditional concepts of regulation involving winter forage supplies. Alternatively, regulation involved intraspecific interactions that influenced use of habitat during late spring and summer and fawn survival to early autumn. Implications for management of the population and its habitat are discussed.

INTRODUCTION

White-tailed deer are widely distributed across the northern Great Plains where they now occupy a wide spectrum of habitats--from foothills on the east slope of the Rocky Mountains to bottomlands along rivers and streams, timbered uplands, and shortgrass prairie. Although commonly associated with agriculture, especially in portions of the region characterized by semiarid climate (Allen 1971, Swenson et al. 1983, Herriges 1986), they can also be found in habitats where agriculture has only negligible influence (Dusek 1987).

Historically, whitetails primarily inhabited river bottoms in the northern plains (Allen 1971). Though gradually extending their range to other habitats in relatively recent times, bottomlands along major rivers continue to be a stronghold of the species throughout the region. Nearly half of all white-tailed deer in southeastern Montana winter in riparian habitat along streams (Swenson et al. 1983). Similarly, riverine habitats typically support much higher densities of whitetails than adjacent prairies.

Population characteristics and dynamics of deer may vary in relation to physical and biological characteristics of individual habitats (Cheatum and Morton 1946, Gill 1956, Dapson et al. 1979, Mackie 1983) but few comparative data are available. Long-term research on population ecology of white-tailed deer has been limited largely to penned or confined populations (Arnold and Verme 1963, McCullough 1979, Woolf and Harder 1979). Published studies of natural, free ranging populations are limited to chaparral shrublands of the Southwest (Teer et al. 1965), mixed conifer-deciduous forest of the upper Midwest (Hoskinson and Mech 1976, Nelson and Mech 1981, 1984), and the tidelands of the lower Columbia River (Gavin et al. 1984).

Our study on population ecology of whitetails along the lower Yellowstone River was initiated in 1980 as part of a broad, long-term research effort to determine and compare population ecology and habitat relationships of deer among the major habitats in which they occur in Montana. That effort, which began in 1975, was precipitated by the inability of existing knowledge to explain widespread declines in deer populations, especially mule deer (*O. hemionus*), across the state during the early 1970's. Comparative studies offered the best opportunity to determine the relative influence of various potential limiting factors. In addition, the lower Yellowstone River offered an opportunity to study relationships between stream dynamics, riparian habitat, and white-tailed deer populations. These data were required in efforts to maintain an instream flow reservation of water in the Yellowstone River for the benefit of fish and wildlife. The Yellowstone River is unique in being one of the last large rivers in the lower 48 states that remains free-flowing in its entirety.

Data were collected from February 1980 through October 1986 with emphasis on factors affecting population size and trend and habitat use relationships. Specific objectives were: (1) to determine ecological and biological parameters associated with a major river bottom population of white-tailed deer; (2) to relate those parameters to environmental characteristics and specific factors potentially limiting deer populations, including nutrition, land use practices, climate, and natural and man-caused mortality; and, (3) to develop methods, criteria, and guidelines for management of deer and their habitat in riverine environments. Our approach was two-fold: extensive studies of population characteristics and dynamics and habitat relationships along an entire segment of the lower Yellowstone River; and, intensive studies within specific units.

STUDY AREA

The lower Yellowstone River extends 350 km, from the mouth of the Bighorn River east of Billings, MT, to the confluence of the Yellowstone and Missouri Rivers in western North Dakota. The study area included 79 km (224 km^2) of floodplain and islands of the lower Yellowstone between Interstate-94 at Glendive and Montana highway 23 near Sidney (Fig. 1). The river is paralleled by Montana highway 16 on the northwest side throughout the entire length of the study area and by the U.S. Bureau of Reclamation (USBR) Canal from Intake to Sidney.

The lower Yellowstone River traverses both glaciated and unglaciated portions of the Missouri Plateau in the Great Plains Province (Fenneman 1931). The landscape of the region slopes gently eastward. Physiographic features consist of rolling uplands, alluvial deposits, and a terraced floodplain to the northwest of the river, and high benches and/or rugged "badlands" immediately adjacent to the river channel on the southeast side. Width of the floodplain varies from 2 km immediately upstream from Intake to 7 km south of highway 23 (Fig. 1). Sandstone, shale that includes some outcropping of clinker or "scoria", and coal seams of the Fort Union Formation are intermittently exposed along the Yellowstone Valley. Elevations on the river vary from 625 m at Glendive to 577 m at Sidney.

The length of the main channel in the study area is 101 km with an average sinuosity of 1.3 (Hinz 1977). Mean stream discharge normally peaks in June (1,121 m^3/second) and drops off from July (662 m^3/second) to August (223 m^3/second) (Moore and Shields 1980). Major flooding caused by ice jams occasionally occurs along the floodplain during February or March.

Soils of the study area are deep, fine sandy loams and silt loams on the low terraces and floodplain and silty clay loams on

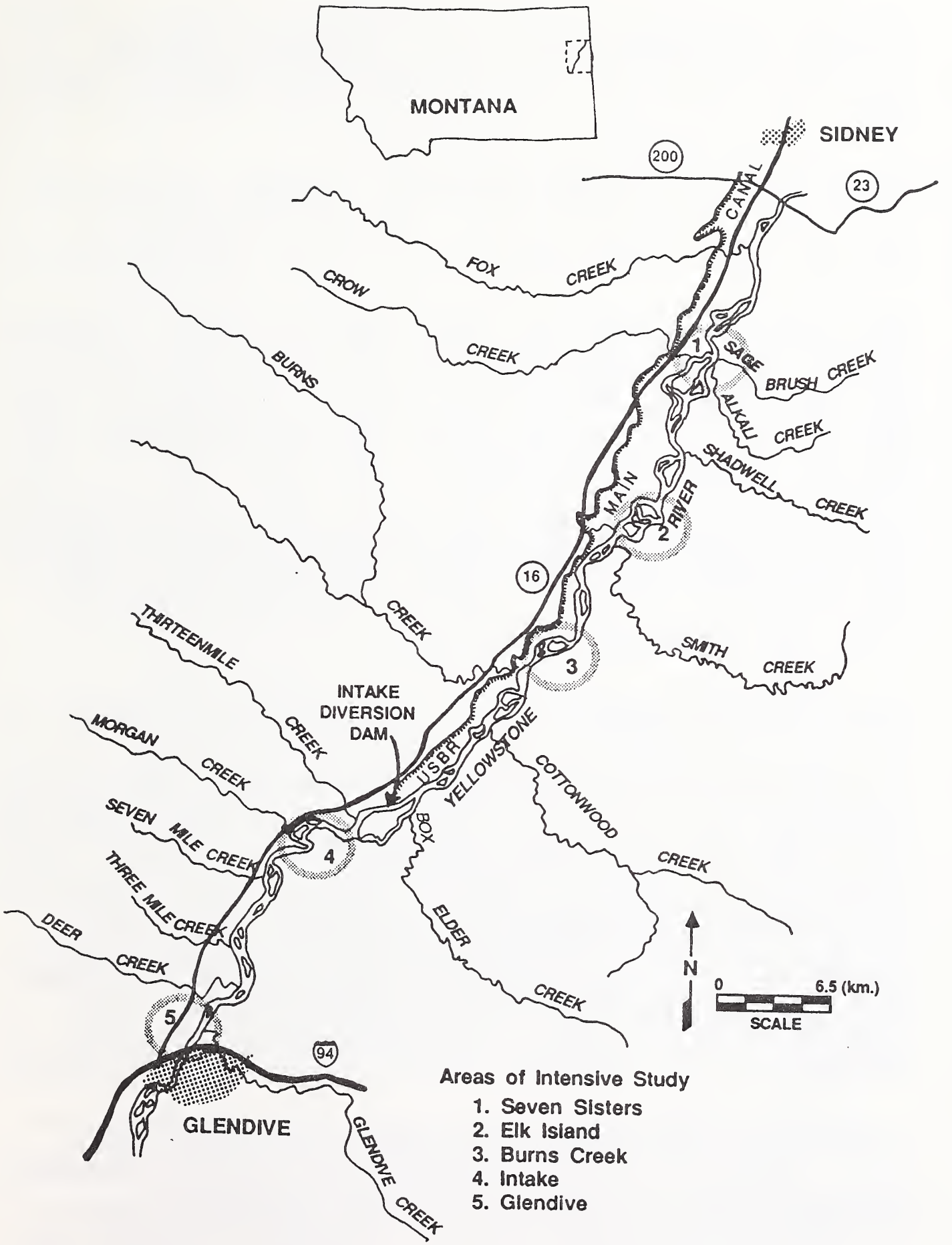


Figure 1. The lower Yellowstone River study area.

alluvial fans and upper terraces (Holder and Pescador 1976, Pescador and Brockman 1980). Soils of adjacent dissected sedimentary plains vary from deep silt loams to gravelly sands underlain by silty clay sedimentary beds or a thick layer of sand.

The regional climate is semiarid with marked variation in seasonal precipitation and temperature. Weather data for the study area (Table 1, Fig. 2) were from official records for Sidney, Savage, and Glendive (U.S. Dep. Comm. 1979-86) with longterm average values based on data for the years 1951-80.

Mean annual precipitation in the region is about 35 cm of which approximately 80% falls during April-September. Sidney and Savage receive slightly greater annual precipitation than Glendive, although monthly means are variable between locations and highly variable between years (Table 1). Mean annual precipitation between the 3 stations varied during 1979-85 from 78 to 82% of the long-term average. Precipitation was above the long-term average only in 1982.

The warmest and coldest mean daily temperatures are recorded in July and January, respectively (Fig. 3). Average monthly temperatures are increasingly cooler with distance north from Glendive. Monthly mean temperatures at Glendive average 2.3 C warmer than those at Sidney. The frost-free period along the valley floor at Glendive is 130 days.

Winter weather, characterized by subfreezing mean daily temperatures and periodic snowfall, may begin during November and persist through March (Fig. 3). Average annual snowfall along the lower Yellowstone Valley is about 71 cm; significant accumulations are rare. Trends in winter severity, based on an index that considered the cumulative effects of winter weather on the condition of free-ranging deer using concepts of Leckenby and Adams (1986), for only Sidney and Savage appear in Table 2. By comparison, the winter of 1981-82 was the severest during the period of study, but less severe than 1978-79. The winters of 1979-80, 1980-81, and 1982-83 were comparatively warm and snowfree. Winter 1983-84 was characterized by abnormally cold temperatures and complete snow cover during December through mid January followed by above average temperatures and snow-free conditions through February. Temperatures and precipitation approximated long-term averages during the winters of 1984-85 and 1985-86.

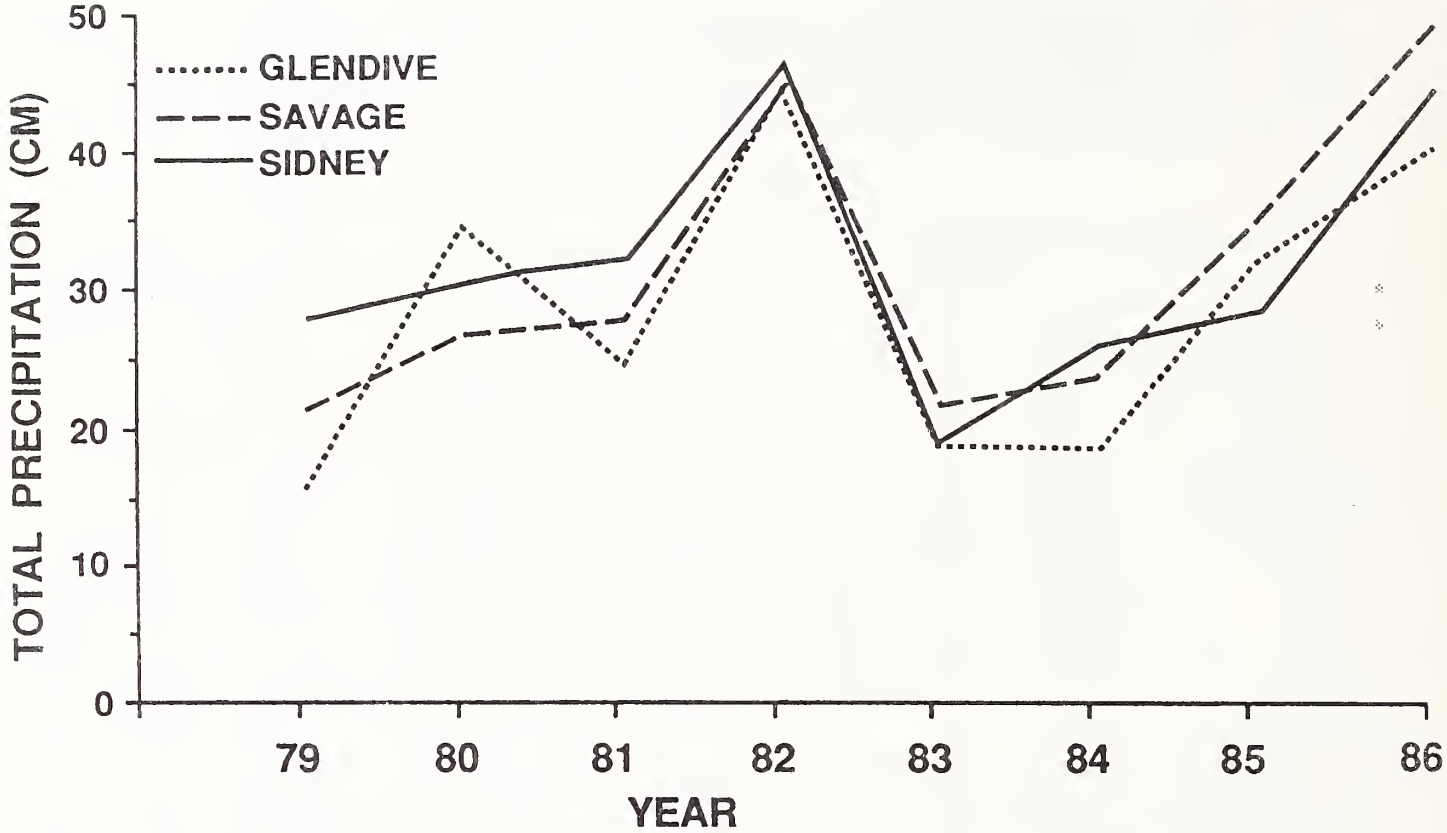
Major riparian communities along the lower Yellowstone were identified and successional relationships described by Boggs (1984). Communities include young cottonwood, mature cottonwood, shrub, grassland, willow-shrub, green ash (Fraxinus pennsylvanicus), and peach-leaved willow (Salix amygdaloides). The grassland sere that dominates the floodplain originates with plains cottonwood (Populus deltoides) and sandbar willow (S. fluviatilis) seedlings colonizing recently formed sand and gravel bars. The willows disappear after approximately 20 years. The

Table 1. Monthly precipitation data for 3 reporting stations on the lower Yellowstone River including 30-year (1951-80) means (N), and 7-year means ($\bar{X}$), and coefficients of variation (CV) for the calender years of 1979-85.

	Precipitation by Station (cm)								
	Sidney			Savage			Glendive		
Month	N	$\bar{X}$	CV	N	$\bar{X}$	CV	N	$\bar{X}$	CV
January	1.02	1.00	91%	0.94	0.71	109%	1.14	0.74	99%
February	1.02	0.69	108%	0.79	0.51	130%	1.04	0.46	139%
March	1.19	1.68	87%	1.09	1.59	102%	1.14	1.68	84%
April	3.05	2.17	68%	3.27	2.04	63%	2.97	1.63	73%
May	5.33	2.74	67%	5.26	3.85	88%	5.18	3.39	82%
June	7.06	5.53	57%	8.23	5.77	70%	7.95	4.97	57%
July	4.47	4.38	48%	4.98	3.27	59%	4.37	2.78	67%
August	4.14	3.64	75%	3.86	3.55	72%	3.40	4.14	108%
September	3.28	2.89	43%	3.25	2.63	47%	2.92	2.22	72%
October	1.98	3.22	91%	1.78	3.09	89%	1.72	2.81	81%
November	1.19	0.88	56%	0.91	0.62	71%	1.16	0.66	76%
December	1.07	1.22	71%	0.84	1.24	45%	1.04	1.13	59%
Total	34.80	30.04	--	35.2	28.87	--	34.03	26.61	--

resulting young cottonwood community is characterized by a maximum canopy height of 20 m and a relatively sparse understory of grasses. Cottonwoods continue to mature and reach a maximum height of about 25 m. The mature cottonwood community is characterized by widely spaced trees and a dense understory of shrubs and herbage. Cottonwoods disappear after approximately 100 years, leaving a shrub community dominated by western snowberry (Symphoricarpos occidentalis) and Woods rose (Rosa woodsii). Herbaceous cover in the shrub community is less than in mature cottonwood stands. Receding shrublands are replaced by grasslands dominated by western wheatgrass (Agropyron smithii) and prairie sandreed (Calamovilfa longifolia). Silver sagebrush (Artemisia cana) is locally abundant throughout the grassland community.

Green ash may first appear in either the young or mature cottonwood stands and ultimately replaces the relatively ephemeral cottonwoods and apparently constituting climax vegetatation on sites capable of continuing to support tree cover. Other tree species occurring with green ash include American elm (Ulmus americana) and boxelder (Acer negundo). Boggs (1984) characterized regeneration of these species as "patchy."



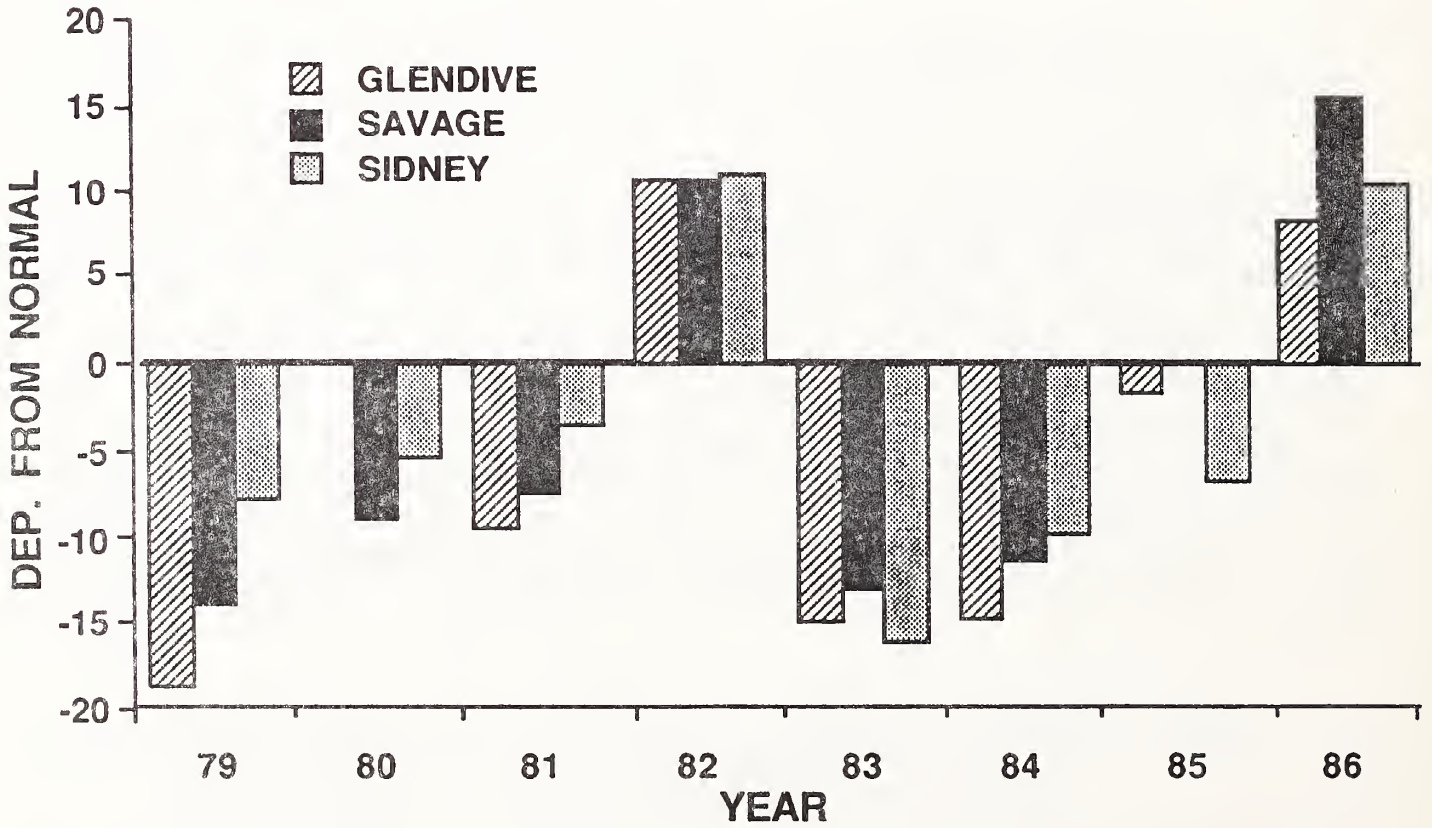


Figure 2. Annual precipitation and departure from the longterm mean (1951-80) at 3 locations on the lower Yellowstone River, 1979-86.

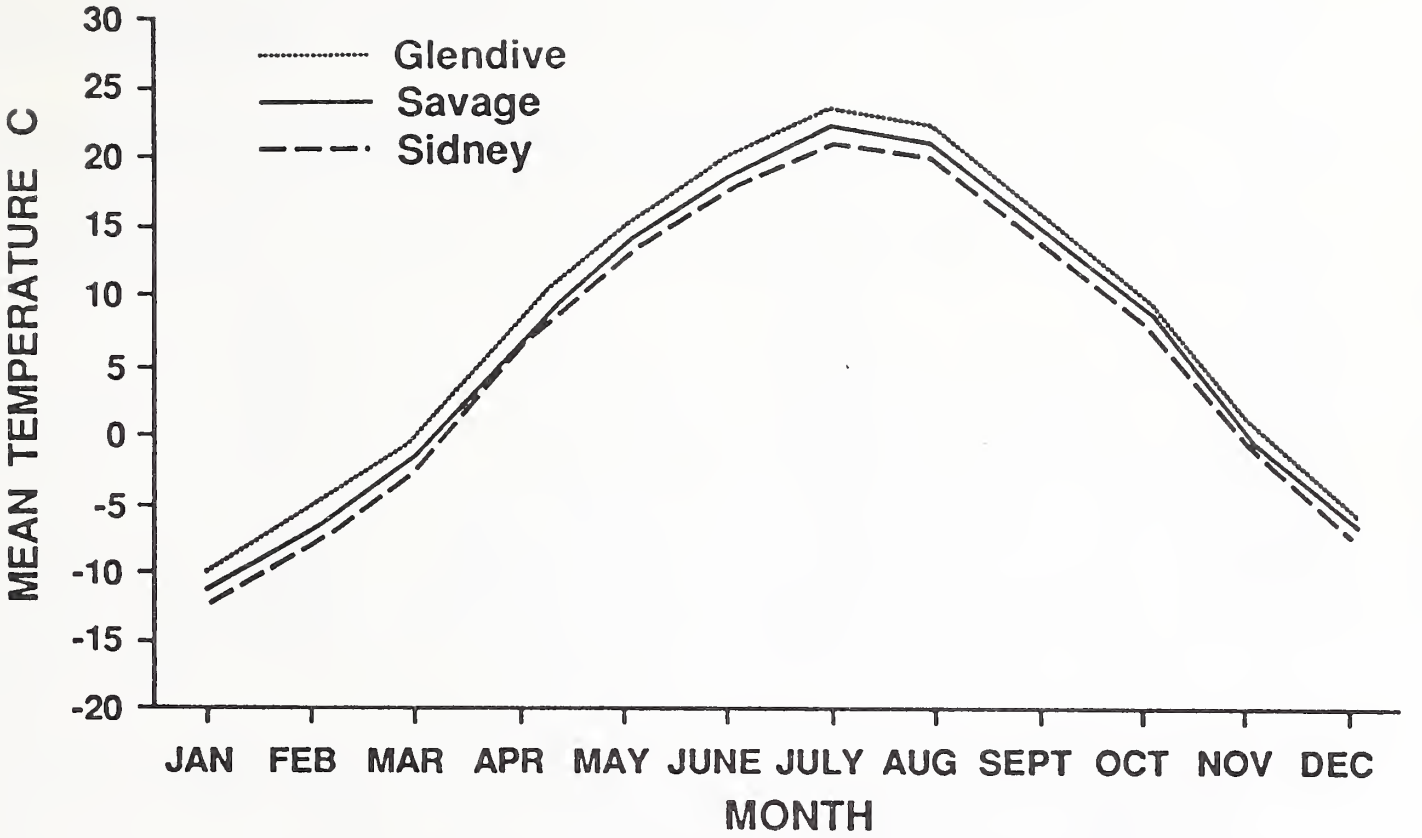


Figure 3. Mean longterm (1951-80) daily temperatures by month at 3 locations on the lower Yellowstone River.

The peach-leaved willow sere becomes established where willows invade newly-formed sand/gravel bars in the absence of plains cottonwood. A green ash community may eventually replace the willows similar to succession in cottonwoods. Marshes occur in ephemeral stream channels, but successional relationships were not determined.

Plant communities in the uplands adjacent to the river bottom were described by Swenson (1982). Mixed grasslands, where western wheatgrass, blue grama (Bouteloua gracilis) and thread-leaf sedge (Carex filifolia) predominate, occur on flat to rolling uplands. Some of the lower side drainages are bordered by badlands characterized by steep, sparsely vegetated slopes. Stands of Rocky Mountain juniper (Juniperus scopulorum) occur along some of the deeply eroded drainages. The more mesic draws support deciduous trees and shrubs that include green ash, boxelder, American elm, and silver buffaloberry (Shepherdia argentea). Cultivated lands on the upland terraces and benches support primarily dryland cereal crops.

Table 2. Winter severity based on a modified Leckenby index for Savage and Sidney, MT, 1975-76 through 1985-86. The index includes 15 November through 31 March.

Year	Winter Severity Index	
	Savage	Sidney
1975-76	1095	1500
1976-77	1053	1393
1977-78	1612	2191
1978-79	1973	3063
1979-80	958	1115
1980-81	710	816
1981-82	1536	2110
1982-83	736	879
1983-84	1090	1238
1984-85	1058	1164
1985-86	1119	1409

Land Uses

The lower Yellowstone served as a route of travel by Indians, trappers, and traders prior to settlement in the late 1800's (Brown 1961). The area was first settled by cattlemen during the late 1870's. Extensive homesteading occurred between 1900-30. The area includes several small rural communities established during the homestead era or construction of the Lower Yellowstone Project: Crane, Savage, Intake, and Stipek. Human population has dwindled since the 1930's in all but Savage.

Irrigation of native meadows that involved spreading water with simple diversions also began during the early 1900's as a result of low production or failure of native hay during dry years. Construction of the Lower Yellowstone Project began in 1905 with water available in 1909. The project was built to irrigate 224 km^2 (56,000 acres) of floodplain and terraces downstream from Intake; however, the potential for irrigated farming lay dormant until production of sugar beets became important in the local economy in 1925 (Mercier 1985). Agriculture is the principal land use along the lower Yellowstone Valley and includes production of livestock, forage, and cash crops. The floodplain on the northwest side of the river downstream from Intake that is flood irrigated from the Lower Yellowstone Project (USBR main canal, Fig. 1) is the most intensively farmed portion of the study area. Sugar beets, alfalfa, corn, and small grains are the principal crops. Untilled portions of the floodplain are grazed by livestock.

Livestock forage, including corn and hay crops, is produced on a few bottomlands on the southeast side of the river. These occur primarily where ephemeral streams enter the Yellowstone. Water for irrigation is provided by private pumping systems.

Most of these bottoms are also grazed, at least during fall and/or winter.

Production of livestock and forage crops are the principal land uses on the floodplain above Intake. Small grains are also produced. Hay crops include alfalfa and native and introduced grasses. Most areas are grazed during fall and/or winter, although they may also be grazed during abnormally dry summers when forage production in the uplands is poor.

Although some oil production structures occur on the floodplain near Sidney, recreation, including hunting, fishing, boating, and searching for agates, is the only other major land use. Because of their isolation and relative inaccessibility, few islands on the river receive agricultural use. Their major use is by recreationists. The Montana Department of Fish, Wildlife, and Parks (MDFWP) owns and manages 2 parcels of land that include both floodplain and islands. These areas are managed for wildlife habitat and recreation, including access to the river.

In 1978, the MDFWP was granted an instream reservation of water in the Yellowstone River under the 1973 Montana Water Use Act that recognized fish and wildlife as beneficial uses of water. This reservation, 5.5 million acre/feet at Sidney, constitutes a flow that can be expected to be equalled or exceeded in 85 of 100 years.

Intensive Study Units

Initially, 3 areas that reflected variation in kinds and intensity of agricultural cropping were selected for intensive study. The Elk Island and Seven Sisters units represented segments of river bottom influenced by the lower Yellowstone Project downstream from Intake (Fig. 1); the Intake unit represented bottomlands above Intake where livestock production and dryland farming are the principal land uses. Intensive effort was extended to two additional areas in 1984, primarily to further quantify factors influencing deer distribution (Compton 1986b). These were near the mouth of Burns Creek and immediately below Glendive (Fig. 1). Size, amount of riparian cover, and relative agricultural usage of intensive study areas are summarized in Table 3.

The Elk Island unit is located in Richland County approximately 26 km downstream from the Intake diversion dam (Fig. 1). It includes the MDFWP-owned Elk Island Wildlife Management Area (EIWMA) and surrounding private lands northeast of the community of Savage. The EIWMA also includes some agricultural land. The floodplain is bounded on the northwest by a broad terrace that is also irrigated from the Lower Yellowstone Project, and on the southeast by steep bluffs and badlands. Principal crops include sugar beets, corn, small grains, pinto beans and hay. A portion of the area is grazed by sheep. The

Table 3. Total area, riparian cover (forest and shrubland), agricultural croplands, and grazing intensity in each of 5 study units on the lower Yellowstone River.

Study Unit	Total Area	Riparian Cover Area	Agriculture Area	Grazed[a] Area
Seven Sis.	23.92	9.47 (0.40)[b]	5.82 (0.24)	8.16 (0.34)
Elk Isl.	24.30	8.69 (0.36)	9.23 (0.38)	8.45 (0.35)
Burns Cr.	13.58	4.93 (0.36)	3.93 (0.29)	7.23 (0.53)
Intake	36.21	8.61 (0.24)	7.87 (0.22)	32.45 (0.90)
Glendive	7.43	2.25 (0.30)	2.14 (0.29)	4.44 (0.60)

[a] The portion of each study unit that is grazed by livestock may include either or both the agricultural and riparian components.

[b] Areas are km^2 (proportion of total area).

only floodplain area on the southeast side of the river in the unit occurs where Smith Creek enters the Yellowstone. This area includes irrigated hay meadows and is grazed by cattle during fall, winter, and spring. A relatively small proportion (35%) of the entire unit is actually grazed.

The Seven Sisters unit that includes some floodplain and Seven Sisters Island lies west of the small community of Crane approximately 39 km downstream from the Intake diversion dam. The unit includes the Seven Sisters Wildlife Management Area (SSWMA) and surrounding private lands. Cropping practices are similar to Elk Island in that floodplain northwest of the river is flood irrigated from the Lower Yellowstone Project. The southeast side of the river also includes floodplain on which livestock grazing and hay production are the principal land uses. As at Elk Island, livestock grazing, which affects 34% of the area is a minor land use overall (Table 3).

The Intake unit lies immediately upstream from the diversion dam in Dawson County (Fig. 1). The area is almost exclusively in private ownership with the exception of one island administered by the Bureau of Land Management (USDI). Nearly all of the unit is grazed by livestock (Table 3). Floodplain areas are grazed by cattle during fall and winter. Irrigated hay crops including alfalfa are also grown on the floodplain. Small grains including winter wheat and barley are grown under dryland farming practices on the floodplain and on adjacent terraces. The southeast side of the river floodplain is bounded by a terrace and rolling uplands dissected by several hardwood draws. Badlands occur on the northwest side of the floodplain.

The Burns Creek unit (Fig. 1) lies approximately 16 km downstream from Intake. Although irrigated crops were grown on more than one-third of the unit, over one-half of the area was grazed by livestock (Table 3). Bottomlands were grazed primarily during late fall and winter.

The Glendive unit abutted the southern boundary of the study area approximately 21 km upstream from Intake. Sixty percent of the unit was grazed by livestock with most cultivated and irrigated lands used for production of hay crops.

METHODS

A total of 426 deer was captured and marked on the Elk Island, Seven Sisters, and Intake units during 1980-86; 39 deer were captured and marked at Burns Creek and Glendive during 1985. Most were captured from late December through early April with Clover traps (Clover 1954) or cannon nets (Hawkins et al. 1968). Six were taken with a hand-held net gun (Barrett et al. 1982) on the Intake unit during February 1984. We assume that trap placement using a combination of techniques over time provided representative samples of the population.

Captured deer were manually restrained. Sex, age determined by tooth replacement and wear (Severinghaus 1949), and general condition were noted for each. During 1984-86, a blood sample was taken and, when practicable, heart girth was measured. A numbered metal ear tag was attached to each ear of all deer, 141 were equipped with transmitter collars, and the remainder were marked with 10-cm-wide individually recognizable vinyl neckbands.

Relocation of radio-collared deer employed a PA-18 Super Cub aircraft. Each radio-collared deer was relocated 2-3 times per month during June-November and 1-2 times per month during December-May. A visual search was made for each animal. The animal's location, cover type occupied, and time of day to the nearest 15 min. were recorded. Deer with individually recognizable neckbands were observed incidental to relocating radio-collared deer, during population census and herd composition surveys, or during other reconnaissance. The number of fawns observed at-heel with marked females was recorded during June-October. A sample of 368 marked deer provided 5,877 relocations during diurnal and crepuscular periods from March 1980 through May 1986.

During summer 1982 and 1983 and winter 1984, hourly relocations of radio-collared deer were also obtained throughout the diel period at Elk Island and Intake by triangulation (Heezen and Tester 1967). This employed stationary or truck-mounted antenna arrays as described by Herriges (1986). A total of 5,648 usable locations were obtained.

Population characteristics were determined from aerial surveys designed for census following rationale and procedures described by Mackie et al. (1981) and Rice and Harder (1977). Basic surveys were conducted from a fixed-wing PA-18 Super Cub during October, late December-early January, and late March-early April of each year. All employed the same pilot and observer and were flown in a manner to provide complete coverage in areas within predictable survey units. Autumn surveys consisted of a single flight over study units where marked deer were present, except during 1984 and 1985 when the entire river bottom study area was flown. Early winter surveys consisted of a single flight covering the entire river bottom during each of the 6 years. Early spring surveys consisted of 2-3 replicate counts of study units where marked deer were available. In addition, the Elk Island and Burns Creek study units were surveyed with a Bell 47G helicopter during February 1984-86 and February 1985, respectively. Numbers, sex and age when practicable, and the number and identification of marked deer observed were recorded and locations plotted on aerial photographs.

From aerial surveys during autumn and early winter, deer were classified as fawn (<12 months of age), adult female, yearling (12-24 months of age) male and adult male. Yearling and older males were generally differentiated by gross differences in antler size. No attempt was made to differentiate yearling and older females. Abundance of females older than fawns and males older than yearlings in autumn populations was estimated from samples of hunter-killed and live-trapped deer by assigning individuals to their respective cohorts for each year that they occurred in the population. We assumed the 2 sexes of fawns to occur in equal proportion during autumn. Deer within individual cohorts were assigned to successive age classes on 1 June. During spring aerial surveys, individual deer were classified as adult or fawn.

Annual population estimates for the river bottom study area were developed from counts during early winter surveys. Particular emphasis was given to data for 1981-82, 1982-83, and 1985-86, years of optimal observability and numbers and distribution of individually marked deer. For each year, survey efficiency was calculated as the mean proportion of individually marked deer observed among intensive study units and applied to the base count derived from an initial population estimate. Population estimates for other seasons and years were extrapolated both forward and backward in time from estimates of mortality and recruitment using change-in-ratio procedures (Downing 1980), documented mortality of marked deer, and periodic aerial surveys. This resulted in 3 estimates for early autumn, early winter, and spring of each year that were then averaged.

Base population estimates for the Elk Island and Intake units were calculated using a Lincoln index (Davis and Winstead 1980) with an average of 12% and 6% of the respective populations marked during fixed-wing aerial surveys in March and April, 1981-86 and for the Burns Creek unit during February and March 1985.

Estimates of numbers and variance from 2-3 flights over each area followed the multiple sampling technique of Rice and Harder (1977). Lincoln index estimates were also made for the Elk Island unit from a single helicopter flight during February in each of the years, 1984-86, and in the Burns Creek unit in 1985. This allowed comparison of population trend and dynamics in areas of contrastingly different land use practices.

Biological material was taken from deer carcasses obtained from several sources: special collections, depredation kill permits, highway mortalities, trap mortalities, hunter harvest, and occasionally, various other mortalities. Sex, age, location, and cause of death were noted for all carcasses. Ages were assigned to all animals by tooth replacement and wear (Severinghaus 1949), and a middle incisor was extracted from those 2 years and older for cementum analysis (Gilbert 1966).

Mean whole weights of white-tailed deer from the lower Yellowstone River were compared during autumn, winter, and late winter/early spring. Whole weights for autumn were estimated from field-dressed weights of 129 deer handled at checking stations and in the field during 1980-85 from a regression of whole to dressed weights of 26 individual deer. Weights for early winter and late winter/early spring were from heart girth measurements (Smart et al. 1973) of 138 live-trapped deer during winters of 1983-84, 1984-85, and 1985-86.

Kidneys and attached perirenal fat were taken from carcasses that were not badly decomposed. The kidney fat index (KFI) was used to evaluate trends in accumulation and mobilization of body fat from 153 deer examined from 1980 to 1986. Procedures for determining the KFI followed Monson et al. (1974). A factorial ANOVA was used to determine the effects of season, sex, age, and study unit (Elk Island and Intake) and the various interactions on the KFI. Summer data were analyzed in a separate ANOVA to compensate for the absence of data for fawns during this season. A least significant difference procedure was used to determine individual differences.

Diastemal length and antler main beam length were recorded for yearling males examined during autumn hunting seasons and used as indexes of condition (French et al. 1956, Reimers 1972). Dressed weights were obtained from hunter-killed deer examined at check stations, while both whole and field-dressed weights were obtained from 26 deer during autumn, winter and spring.

Breeding and fawning dates were estimated from assigned ages of fetuses from 38 females necropsied from January through April. Fetal ages assigned from forehead-rump measurements, based on growth rates of known age fetuses (Cheatum and Morton 1946), were inversely related to the Julian date of collection. This bias was also reported by Jackson and Hesselton (1973). We therefore considered fetal weights in addition to forehead-rump length to assign fetal ages following Armstrong (1950). Only the largest fetus in litters was used to assign an age to minimize

differences attributable to litter size. The midpoint in ranges of fetal ages was used to assign ages to individual litters.

The incidence of ovulation (Cheatum 1949) was used to estimate the reproductive potential of the lower Yellowstone population, as also used by Teer et al. (1965) and others. Because most females had presumably completed their breeding cycle by late December, corpora lutea of pregnancy (CLP) were used to estimate ovulation rates. Reproductive tracts were not examined until mid-January. Corpora albicantia were not used because they offer a more subjective estimation of ovulation than the CLP (Golley 1957). Fertilization rates were determined from the ratio of viable embryos to CLP. Pregnancy was determined from 77 necropsied females during all years and by assay of sera from peripheral blood (Wood et al. 1986a) among 113 females captured during 1984-86. Capture-related stress presumably had no measureable affect on pregnancy diagnosis (Wood et al. 1986b).

Postpartum fawn production was determined from observed fawns-at-heel during July-October. Age specific reproductive success, or recruitment to early autumn, was evaluated from fawns-at-heel among individually marked females of known or assigned ages following Mundinger (1981). During 1980-86, 155 individually marked females provided 269 cases of estimated reproductive performance. The sample included 75 (48%) females that were fawns or yearlings at initial capture. Assignment to these age classes on the basis of tooth replacement allowed for minimal subjectivity. Of 80 females, whose ages were assigned on the basis of wear of cheek teeth, assigned ages of 19 individuals were corrected or confirmed by cementum analysis upon death of the animal. Because capture and marking have no known effect on reproductive success of females (Hamlin et al. 1982), age specific rates of reproduction were considered representative of individual female cohorts within a given year.

Annual and seasonal mortality rates were based on differences between population estimates for the respective periods. Summer fawn mortality was interpreted as the percent difference between fetal rates and autumn fawn:adult female ratios. Seasonal and annual rates of mortality were calculated using exponential rates of population change and were reported as finite rates (Caughley 1977). Although an estimate of total annual mortality was calculated for fawns in this manner, annual turnover in the population only considered mortality of individuals older than 4 months of age. Factors influencing population dynamics were determined by correlation analysis using exponential rates of change.

Distribution of deer in the study area was analyzed by multiple regression by dividing the river bottom into 1.6 km segments as described by Compton et al. (1988). Habitat parameters including the amount of riparian cover and the amount of island area were the independent variables. The dependent variable was the number of deer observed per segment during early winter (December-January) aerial surveys from 1981-82 to 1985-86.

All locations of marked and unmarked white-tailed deer were plotted on 1:24,000 topographic quad maps and were assigned Universal Tranverse Mercator (UTM) coordinates. Annual and seasonal home ranges as expressed by minimum convex polygons (Mohr 1947) and average activity radii (AAR, Hayne 1949) were calculated using the TELDAY software (T. N. Lonner and D. E. Burkhalter, Users manual for the computer program TELDAY, Mont. Dep. Fish, Wildl., and Parks, unpubl.).

Monthly movement patterns of deer on the river bottom were evaluated from 1,737 individual monthly AARs from 189 radioed and neckbanded deer observed 2-4 times in at least one month from June 1980 through May 1985 following procedures described by Dusek and Wood (1986). Differences in monthly AARs by month, sex, and age were determined from ANOVA.

Diurnal home ranges were calculated from both fixed-wing aerial telemetry surveys and from triangulation. Annual home ranges included the area normally used by an animal from 1 June through 31 May. Yearlong and/or seasonal diurnal home ranges were computed for 92 individual radio-collared deer from June 1980 through April 1985. The nonparametric Kruskal-Wallis test was used to test for differences between sex and age groups based on AAR. Differences between groups were determined from LSD tests on the ranks of AARs (Conover and Iman 1981). Estimates of total area (polygon) were only reported. Data for individual deer, during years of dispersal, or periods of temporary movement outside of normal home ranges, were excluded from the analysis. Both diel and diurnal home ranges were similarly calculated from houly relocations obtained by triangulation. A detailed analysis was described by Herriges (1986).

Dispersal (Bunnell and Harestad 1983) direction was evaluated using a Chi-square goodness of fit test for circular distributions.

General trends in habitat selection or avoidance followed a use versus availability procedure (Byers et al. 1984) using 4,579 point locations of radio-collared deer pooled from all intentensive study units. The amount of each cover type was also pooled for all units. All riparian forest communities, regardless of seral stage, were combined in the analysis. Availability of habitat components was determined from maps developed from orthophotoquads and color aerial photographs.

A grid cell analysis following Porter and Church (1987) was used to determine which habitats were important to deer and the effects of habitat diversity and interspersion on habitat selection from 4,932 relocations of individually marked deer older than fawns from the Seven Sisters, Elk Island, and Intake areas. The 3 combined areas included 858 computer-generated 9-ha cells with dimensions of 300 m per side. The amount of each cover type, number of cover patches, number of cover types, and the presence or absence of domestic livestock and slough areas

were recorded for each cell. Use versus availability procedures, as described above, were used to determine factors influencing habitat selection by deer. The nonparametric Kruskal-Wallis and multiple comparison tests were used to determine differences in association with habitat complexes by season, and by sex and age. Cells with no observed use during diurnal periods, 1-2 observations, and 5+ observations were used to contrast habitat complexes with no observed use with those receiving occasional use and those used intensively. Response to grazing treatments by sex and age of deer were determined from 2-way classification chi-square tests (Everitt 1977). Similarly, these techniques were used to evaluate the importance of slough areas and seral communities of riparian forest to habitat selection by deer.

Habitat selection and use during diurnal and nocturnal periods of summer and winter at Elk Island and Intake were evaluated from relocation data for radio-collared deer obtained by triangulation. Location data were intersected with digitized habitat files using GEOCALC (W. Hoskins, computer software written for the Interagency Grizzly Bear Study, Bozeman, MT). The program measured area and length of edge of each cover type within a scanning circle of 125 m radius around each location. All seral stages of riparian forest and crop types were differentiated for this analysis. Random or grid points and scanning circles were generated within each unit to test hypotheses of use versus availability. These procedures are described in greater detail elsewhere (Herriges 1986).

Approximately 1 liter of the contents of the rumen of 184 deer that died from all causes except trapping from April 1980 through March 1986 was collected for analysis of food habits (Wilkins 1957). Data were analyzed by month, season, land use patterns, and by sex and age.

Statistical procedures were consistent with Zar (1984) unless stated otherwise. Analyses were conducted using the Statistical Analysis System (Ray 1982) and Montana State University computing services.

POPULATION CHARACTERISTICS

Historical Abundance and Trend, 1804-1950

The journals of early visitors to the lower Yellowstone and other accounts suggest that white-tailed deer were less abundant historically than at the present time. White-tailed deer were commonly observed along the Missouri River and the lower portions of principal tributaries, including the mouth of the Yellowstone River, during the expedition of Lewis and Clark in 1804-1806 (Koch 1946, Burroughs 1961). The occurrence of white-tailed deer was not documented during W. Clark's trip down the Yellowstone River, although accounts of numerous sightings of bison (Bison bison) and elk (Cervus canadensis) were reported (Brown 1961).

Settlement of the northern Great Plains in the 1860's and 1870's indirectly led to near extirpation of big game populations by the 1880's as a result of subsistence and market hunting (Petersen 1984). An occasional sighting of a whitetail, or a hunter taking an exceptionally large buck, on the mainstem or tributaries of the lower Yellowstone around 1880 were reported by Brown and Felton (1955). Yet, more numerously reported sightings of other big game suggested that white-tailed deer were still relatively scarce. Mule deer were the only big game animals observed on riparian bottomlands of the Yellowstone above the mouth of the Bighorn during the late 1940's (U.S. Fish and Wildlife Service 1952), and Allen (1971) indicated that the relatively limited distribution of white-tailed deer in eastern Montana included the extreme lower Yellowstone River in about 1941.

Recent Population Trends

Whitetails increased in both number and distribution since the early 1940's and occupied several habitats in eastern Montana by the 1950's and 1960's (Allen 1971). Lacking accurate census data for white-tailed deer for years prior to the study, estimates of relative abundance and trend for the lower Yellowstone are highly subjective. The best available indicator may be provided by harvest and recruitment trends (Figs. 4 and 5).

Although harvest trends may not be directly correlated with population size, we believe they reflect gross temporal changes in abundance. For example, total harvest of white-tailed deer in administrative region 7, encompassing 83,200 km^2 of southeastern Montana, increased from 1,000-3,000 per year in the mid to late 1950's to 5,000-21,000 in the early-to-mid 1980's. Sharp increases and subsequent peaks in deer harvests occurred in the early to mid 1970's (11,000) and again in the early to mid 1980's (21,000) and were attributed to liberalized antlerless hunting regulations associated with periods of "peak" abundance. Antlerless regulations have a significant impact on annual harvests (J. E. Swenson. 1978. Montana Dep. Fish, Wildl., and

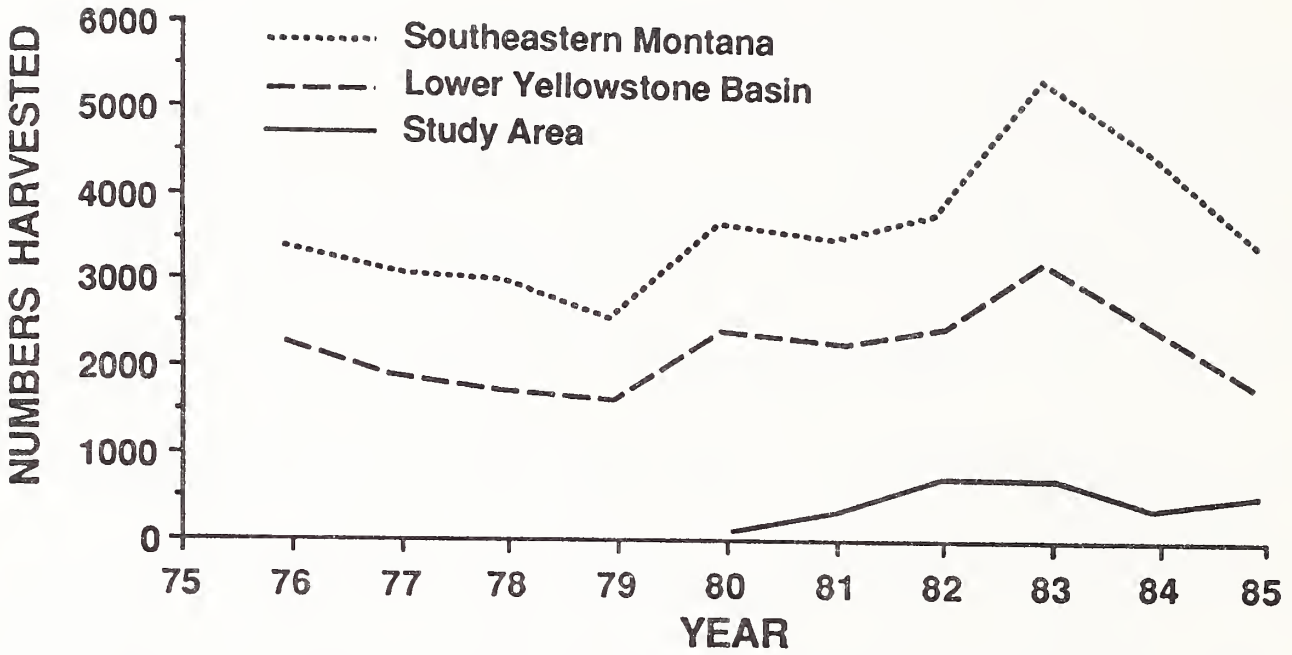


Figure 4. Annual harvests of antlered white-tailed deer in southeastern Montana as reported by the MDFWP (Fed. Aid Proj. W-130-R), 1976-85, and in the lower Yellowstone River study area, 1980-85.

Parks, Fed. Aid Proj. W-130-R, unpubl. rep.).

Harvests in the portion of the region comprising the lower Yellowstone Basin and the divide separating the Missouri and Yellowstone drainages (12,300 km^2), including the study area, followed a similar pattern. The lower Yellowstone Basin accounted for about half of the regional white-tailed deer harvest from 1960 to 1985, while the study area (< 2% of the basin) accounted for approximately 20%.

Trends in harvest of antlered white-tailed deer suggest that the population on the lower Yellowstone River bottom experienced the most recent low point in numbers in the late 1970's (Fig. 4) just prior to initiation of this study. Harvests in the lower Yellowstone Basin and throughout southeastern Montana were lowest during 1979 and highest during 1983. Harvest regulations for antlered whitetails were unchanged during the period of 1976-85, while season lengths and numbers of permits for antlerless deer varied and increased substantially from 1983 to 1985.

Exceptionally high rates of fawn recruitment during 1978 and 1979 (Fig. 5) led to increasing populations throughout the region. Although recruitment declined after 1979, populations continued to increase until 1983.

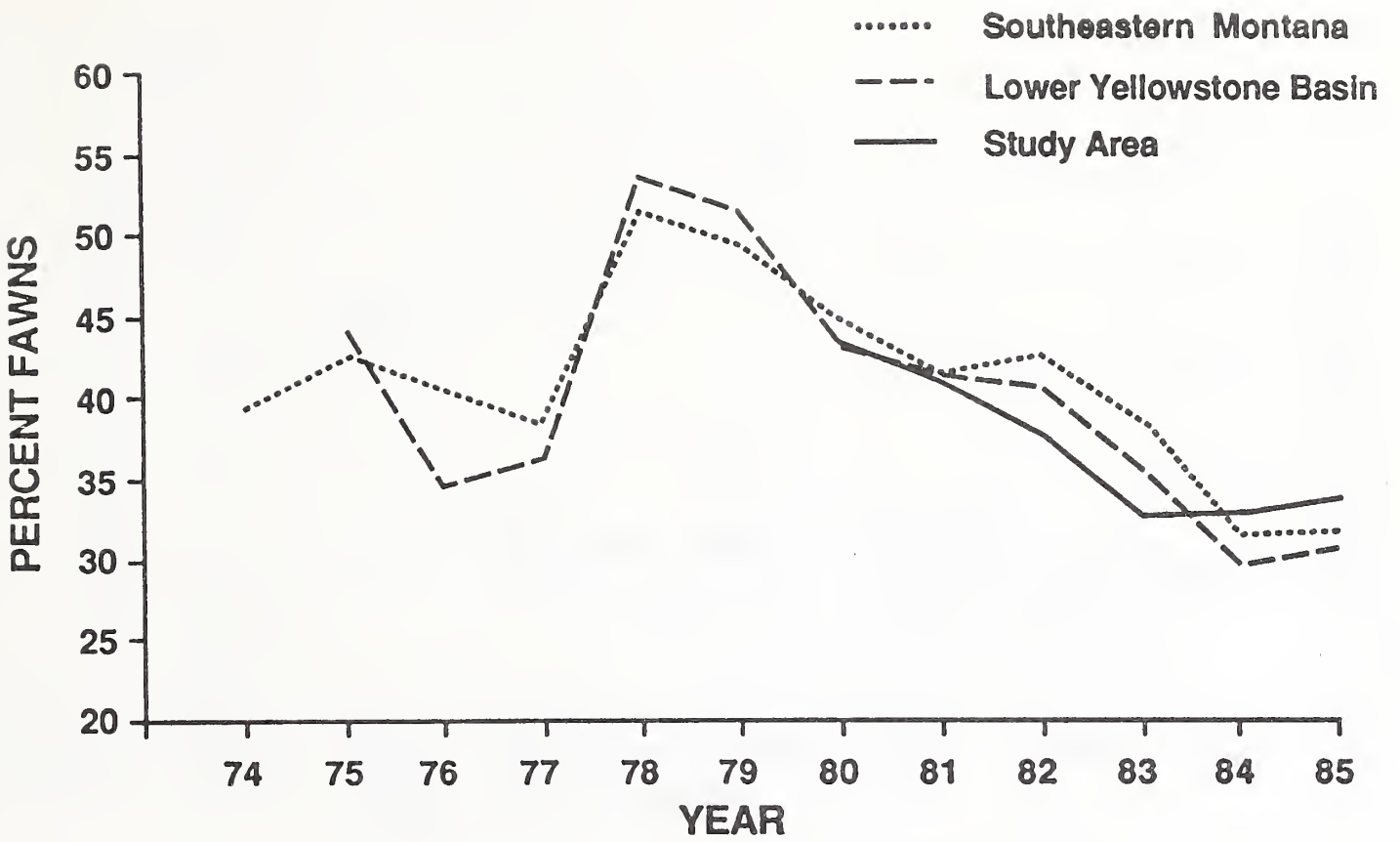


Figure 5. The proportion of fawns in autumn whitetail populations in southeastern Montana as reported by MDFWP (Fed. Aid Proj. W-130-R), 1976-85, and in the lower Yellowstone River study area, 1980-85.

Deer numbers in eastern Montana during 1982-84 may have represented an all-time peak in distribution and abundance for the species in this region (R. J. Mackie et al. 1985. Montana Dep. Fish, Wildl. and Parks, Fed. Aid Proj. W-120-R, unpubl. rep.). Some comparative data also suggested that population size on the lower Yellowstone was relatively high during this study. For example, Swenson (1979) reported a late summer density of approximately 16 deer/km^2 in the Intake area during 1977. An epizootic of hemorrhagic disease (EHD) reduced that population by about 33% by autumn 1977. We estimated early autumn densities of 18-20 deer/km^2 for approximately the same area in 1980 and 50 deer/km^2 in September-October 1983 when population growth had leveled off.

Total deer numbers on the river bottom study area in autumn increased from an estimated 3,100 individuals during 1980 to 5,784 in 1983, then declined to 4,336 by 1986 (Fig. 6). Early winter and spring numbers peaked during 1982-83. Finite rates of change from year-to-year in autumn populations were 42, 25, 4, -5, -13, and -9% for individual years 1980-86, respectively.

Trends in numbers of deer by sex and age (Fig. 7) appeared to reflect declining reproductive success and, in turn, numbers of individuals recruited into successive age classes from 1982

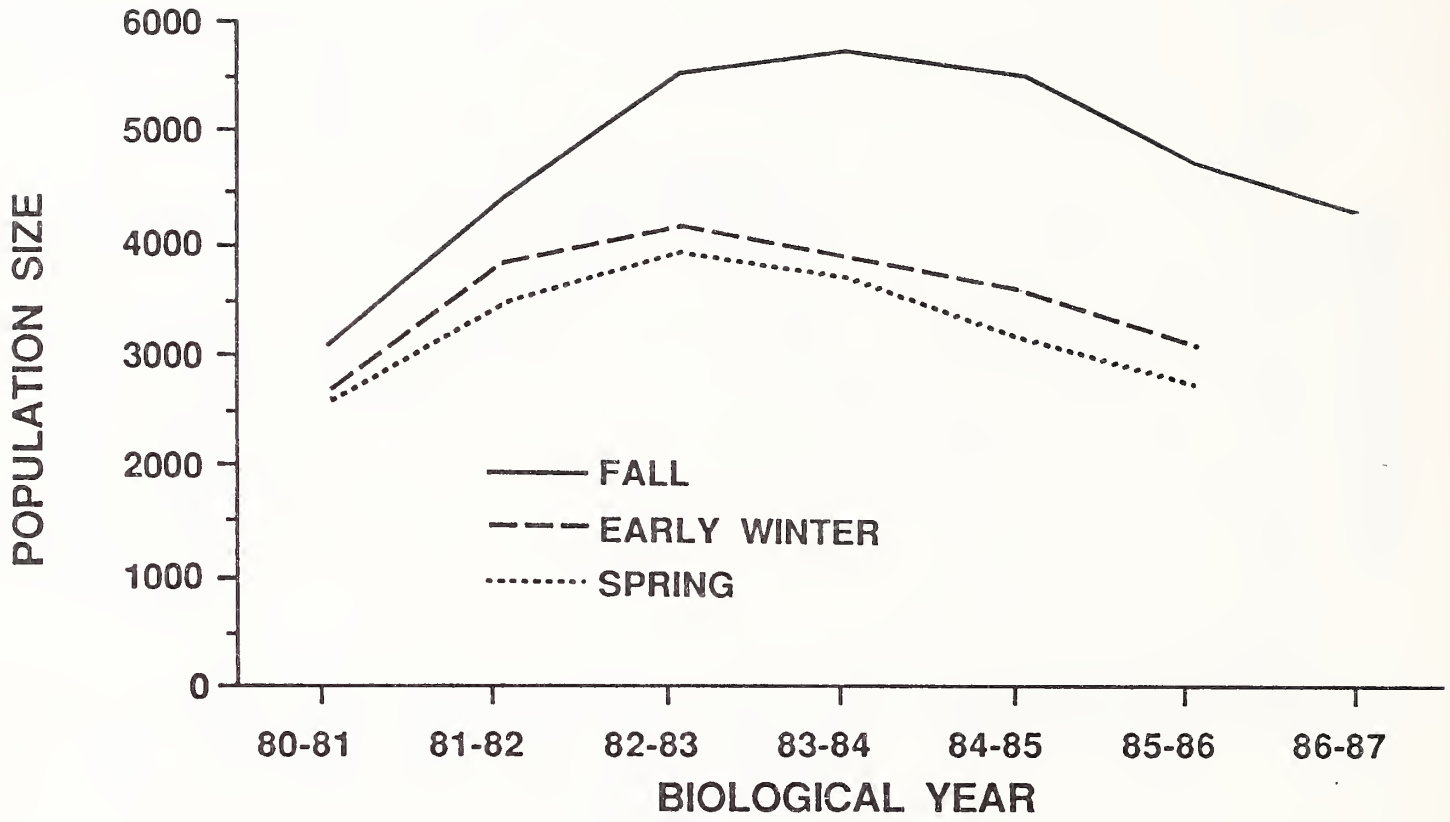


Figure 6. Population trend of white-tailed deer on the lower Yellowstone River, 1980-86.

through 1985. There was a one-year time lag between peak numbers of fawns in autumn populations and peak population numbers. The number of fawns in autumn populations (1,343 in 1980) peaked during 1982 at 2,077 individuals and declined to 1,561 individuals by 1986 (Fig. 7). Numbers of yearlings peaked in 1983 at 1,551. Numbers of adult (2+) females (798 in 1980) increased through 1983 (1,964), leveled off through 1984, and declined through 1986 (1,631). Adult males increased from 1980 to 1982, leveled off through 1984, and increased slightly in 1985, although the total antlered segment that included yearlings declined from 1,263 individuals in 1983 to 767 in 1986.

Spatial Variation in Trend on the River Bottom

Population trend over time differed between segments of the river bottom as exemplified by data for the Elk Island and Intake areas (Table 4). Populations were similar during spring 1981 with a between-area difference of less than 100 individuals. Numbers of deer during spring increased from 1981 to 1984 and declined through 1986 at Elk Island. At Intake, spring population size increased relatively rapidly to 1983, levelled off to 1984, and declined sharply from 1984 to 1986.

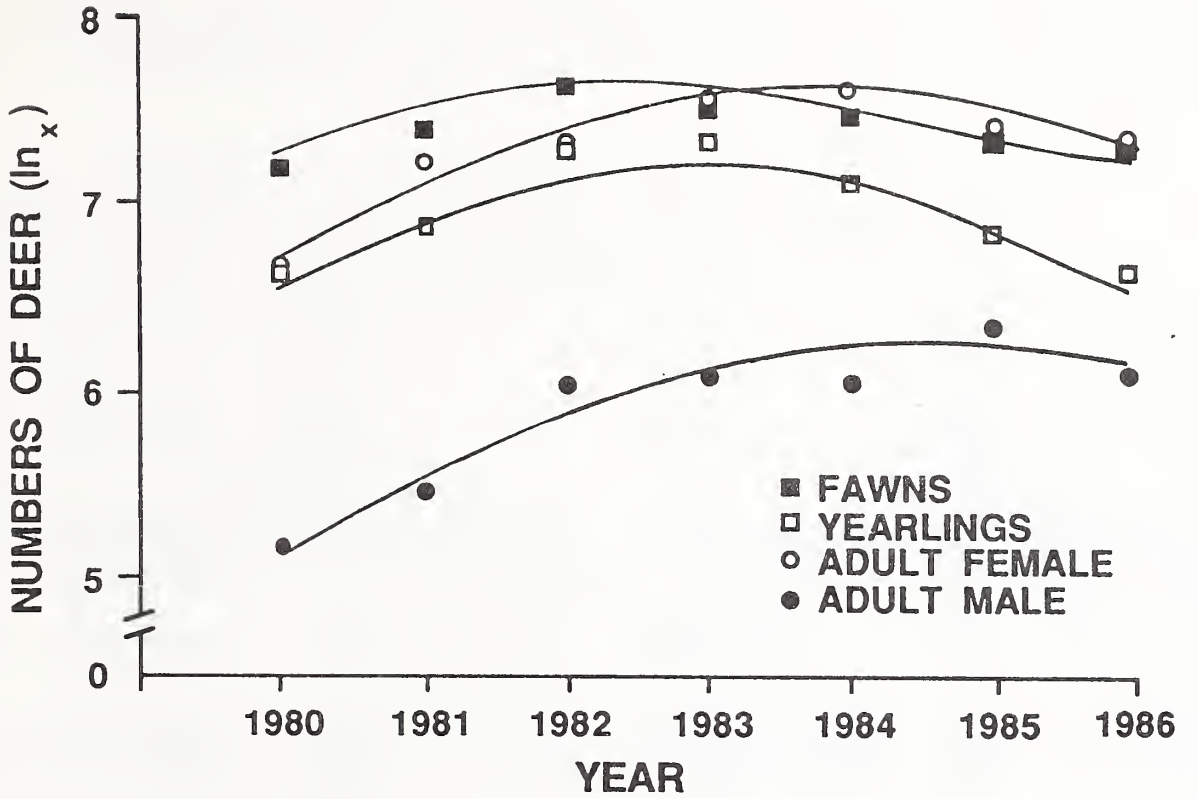


Figure 7. Numbers and trend of white-tailed deer on the lower Yellowstone River by age class, 1980-86.

Population estimates of 654 ±108 ($\bar{X}$ ±SE) and 600 ±96 animals from helicopter surveys at Elk Island in February of 1984 and 1985, respectively, were consistent with estimates from multiple fixed wing surveys in March and April of those years (Table 4). Estimates of 175 ±50 and 173 ±35 deer from one helicopter survey and 2 fixed-wing surveys in the Burns Creek area during February and March 1985, respectively, also indicated consistency between a single helicopter survey and multiple fixed-wing surveys. The differences between estimates for the helicopter survey during February 1986 (434 ±73) and the mean of 3 fixed-wing surveys during March-April 1986 (332 ±84) at Elk Island apparently resulted from redistribution of deer from flooding during an ice jam in late February. Two of 16 transmittered deer had not returned to that area by the time of the early spring fixed-wing census.

Population density was comparatively lower at Burns Creek (12.7/mi^2 than at Elk Island (25.0/mi^2) or Intake (19.9/mi^2). The Burns Creek, Elk Island, and Intake units accounted for 9%, 10% and 14%, respectively, of the total main channel length in the study area. Burns Creek accounted for 5% of total spring numbers in 1985. Numbers of deer at Elk Island and Intake during spring for the years 1981-86 averaged 15% and 18%, respectively, of total numbers in the study area.

Table 4. Population estimates for white-tailed deer in the Elk Island and Intake units from spring 1981-86 using multiple Lincoln estimates and autumn estimates from recruitment of fawns over summer,

	Elk Island			Intake		
Date	Adults	Fawns	Total	Adults	Fawns	Total
Mar/Apr '81	198	190(49%)[a]	388	255	209(45%)	464
Sep/Oct '81	388	259(40%)	647	464	309(40%)	773
Mar/Apr '82	269	179(40%)	448	404	292(42%)	696
Sep/Oct '82	448	299(40%)	747	696	375(35%)	1071
Mar/apr '83	312	266(46%)	578	566	362(39%)	928
Sep/Oct '83	578	285(33%)	863	928	417(31%)	1345
Mar/Apr '84	435	245(36%)	680	638	273(30%)	911
Sep/Oct '84	680	366(35%)	1046	911	354(28%)	1265
Mar/Apr '85	356	183(34%)	539	354	183(34%)	537
Sep/Oct '85	539	330(38%)	869	537	315(37%)	852
Mar/apr '86	236	96(29%)	332	237	102(30%)	339

[a] Percent of total population.

At Elk Island, autumn densities were 26.6, 30.7, 35.5, 43.0, and 35.8 deer/km^2 during 1981-85, respectively. This compared to 28.6, 39.6, 49.7, 46.8, and 31.5 deer/km^2 on the floodplain at Intake during the respective years.

Greater between-year increases, and consequently higher animal density, at Intake than at Elk Island from 1982 to 1983 probably reflected differences in accessibility of the two areas to hunters. Landowners at Intake allowed only limited access to that area until 1984 when more hunting was permitted because of depredation by deer on alfalfa. At Elk Island, the EIWMA provided public hunting during all years, reducing the influence of private landowners on hunter access that apparently minimized year-to-year variation in accessability as well as population density.

Population Structure

General Patterns.--Age structure was pyramidal, comprised largely of younger age classes in both the female and male segments of the population (Fig. 8). An average of 75% (68-79%) of total autumn populations during 1980-85 was 2 years or younger. These age classes included 63% of the females and 93%

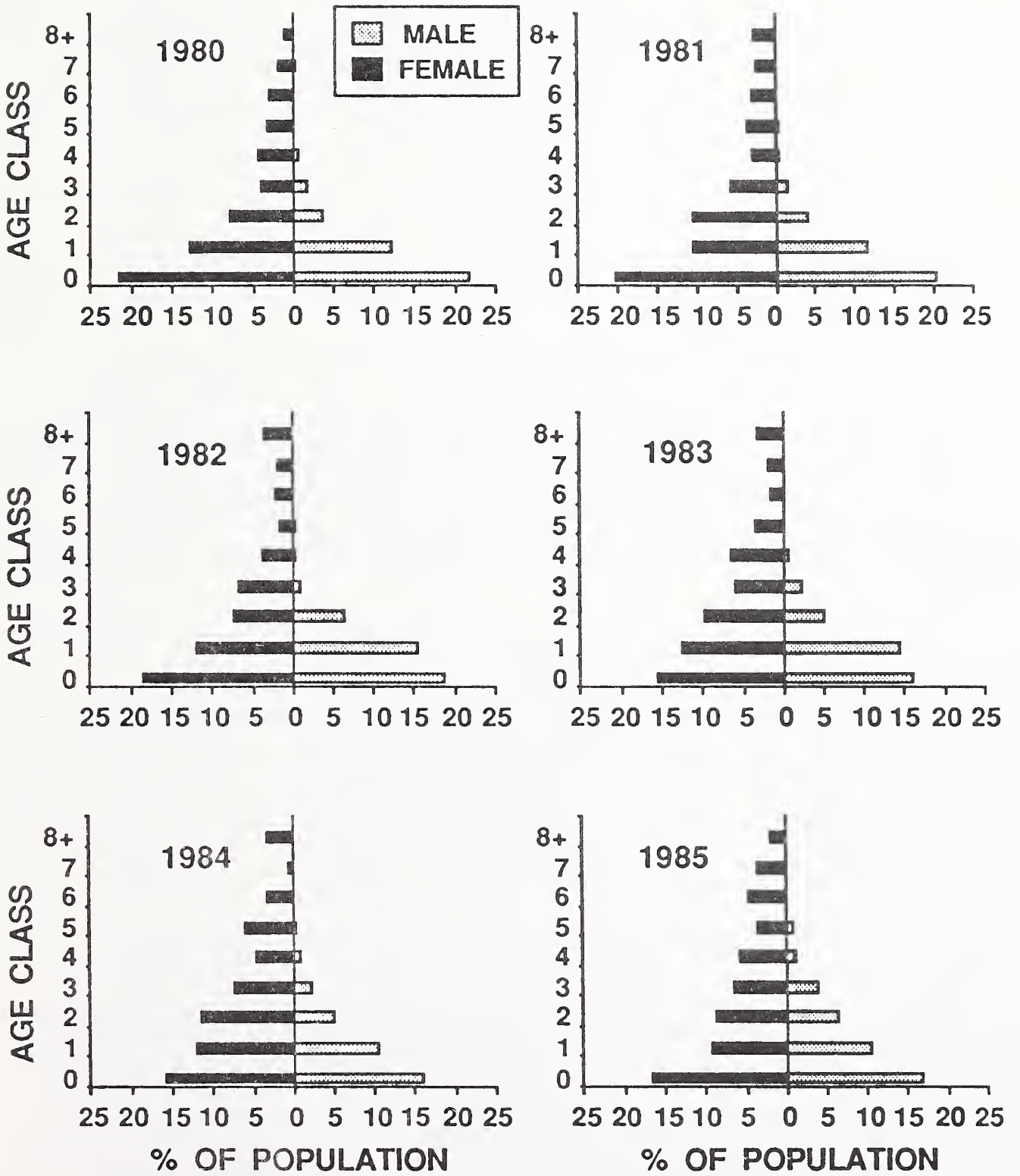


Figure 8. Composition (%) of the whitetail population on lower Yellowstone River during autumn, 1980-85.

of the males. Females 3-7 years old comprised 32% of the female segment, and those 8 years and older 5%. Males older than 4 years comprised less than 1% of the male segment of the population.

Yearling and older females accounted for an average of 44% (39-50%) of pre-hunt populations of early autumn (Table 5). Relative abundance of females in the various cohorts (Fig. 8) suggested that the 1977 cohort (3-year-olds in 1980) was weaker than those of preceding or following years. Conversely, the 1979 cohort (yearlings in 1980) was comparatively strong.

Yearling and older males accounted for an average of 20% (16-23%) of pre-hunt populations (Table 5). Their relative abundance declined sharply from autumn when buck:doe ratios averaged 45:100 (range 37-58:100) to winter when the mean was 25:100 (range 18-37:100).

Fawns comprised 32-43% ($\bar{X}$ = 37%) of autumn populations on the study area during 1980-86 (Table 5). The average autumn fawn:doe ratio was 85:100 and ranged from 64 to 112:100 (Table 5). The relative abundance of fawns declined from 1980 to 1983 and leveled off in 1984, though absolute numbers of fawns added/year increased through 1982 (Fig. 7). Fawns were relatively more abundant in the lower Yellowstone whitetail population than in nearby prairie habitat during the same time period (Wood 1987).

An increase in the proportion of fawns in classifications from autumn to winter during all years except 1984 and 1985 (Table 5) probably reflected disproportionately higher mortality among adult deer during autumn. Trends to spring were confounded by difficulty in distinguishing fawns from adults during late winter and spring. During 1984-85, estimated weights of male fawns and yearling females, trapped during late winter and early spring, overlapped. However, data for both early winter and spring indicated a steadily declining trend in recruitment of young animals into the population from 1980-81 to 1984-85.

Years of high relative abundance of fawns throughout the river bottom coincided with years of low total population numbers. The lower fawn:doe ratios in 1983 and 1984 (Table 5) coincided with years of relatively high population numbers (Fig. 6), whereas the high ratio in 1980 coincided with relatively low numbers of deer. Fawn:adult female ratios of 68:100 and 140:100 were reported for autumn 1977 and 1979, respectively (J. E. Swenson 1978, 1980, Mont. Dep. Fish, Wildl. and Parks, Proj. W-130-R, unpubl. rep). The low recruitment rate for 1977 may have been influenced by the EHD epizootic (Swenson 1979); that of 1979, which was higher than any recorded during this study, coincided with the recent low point in deer abundance.

Table 5. Seasonal herd composition by sex and age of white-tailed deer on the lower Yellowstone River, 1980-86.

Year	Number Classified	% Males 2+	% Males yrl.	% Fem. 1+	% Fawns	Fawns: 100 Fem. 1+	Fawns: 100 Ads. 1+	Bucks: 100 Does
				Autumn (Pre-hunt)				
1980	540	6	12	39	43	112	76	46
1981	334	5	11	43	41	96	69	39
1982	664	8	15	40	37	95	60	58
1983	316	8	14	46	32	68	46	47
1984	484	8	10	50	32	64	47	37
1985	485	12	10	45	33	75	50	50
1986	452	10	8	45	37	82	59	39
				Early Winter				
1980-81	687	5	10	40	45	112	81	37
1981-82	1581	3	7	46	45	99	82	20
1982-83	1089	2	6	47	44	92	78	18
1983-84	1562	3	6	52	39	75	63	18
1984-85	849	4	9	54	33	60	48	25
1985-86	531	6	10	53	31	58	44	31
				Early Spring				
				---% Adults---				
1981	425			55	45		81	
1982	490			59	41		68	
1983	563			58	42		73	
1984	803			67	33		48	
1985	490			73	27		37	
1986	414			71	29		42	

Longevity of females in the lower Yellowstone population was approximately twice that of males (Fig. 8). The oldest ages assigned to females were 13-15 years; the oldest male was 7. Expected ecological longevity of both sexes of deer, determined by wear on the cheek teeth, is about 13 years (McCullough 1979). Greater longevity of females than males may be related to physiological stress imposed on males by breeding (Woolf and Harder 1979, Gavin et al. 1984) and/or other factors favoring female survival such as hunter selectivity (Roseberry and Klimstra 1974).

Spatial Variation.--Fawns were relatively more abundant at Elk Island than at Intake during autumn of all years except 1980 (Table 6). Fawn:doe ratios at Elk Island averaged 99:100 (CV=18%) and ranged from 76 to 118:100; the average for Intake was 78:100 (CV=23%) with a range from 61 to 115:100. Fawn numbers during autumn at Elk Island were less variable than at Intake over time, coinciding with comparatively lower and more stable numbers of adults at Elk Island (Table 4). Coefficients of variation in numbers of adults during autumn were 26% and 37% for the respective areas during 1981-86. For estimated numbers of fawns during the same years, the coefficient of variation was 20% at Elk island and 25% at Intake.

Buck:doe ratios were more variable than fawn:doe ratios. The respective coefficients for buck:doe ratios were 35% and 32%. Some of the variability in buck:doe ratios probably resulted from differential observability between adult males and females (Downing et al. 1977).

Adult males were relatively, though not necessarily numerically, more abundant at Elk Island than at Intake (Table 6). Average buck:doe ratios were 53:100 (range 26-73:100) and 38:100 (range 20-49:100) in the respective segments of river bottom. A year-to-year trend in relative abundance of antlered deer within each unit was not apparent perhaps because of high variability. Some of the difference in mean ratios between areas probably reflected disproportionately different rates of removal of bucks by hunting.

Physical Characteristics

Weight Relationships.--Dressed weights of fawns during autumn averaged 23.5 and 24.1 kg for females and males, respectively. Those of yearlings were 39.6 kg for females and 49.8 kg for males. Dressed weights increased with age to 45.2 kg for females 4 years and older and 74.8 kg for males of similar age.

Field-dressed carcass weights of lower Yellowstone whitetails during autumn were comparable to average weights from hunter check stations from throughout Montana during 1948-63 (Mackie 1964). Whitetails from the lower Yellowstone were slightly heavier than those reported by Wood (1987) from nearby prairie habitat that probably reflected differing effects of environmental conditions of deer in the respective habitats. Mean age-specific field-dressed weights of males and females from the lower Yellowstone were 91% and 87%, respectively, of weights reported for the Swan Valley of northwestern Montana (Dusek et al. 1987). The overall trend may have reflected genetic differences between the 2 populations. However, comparatively lighter weights among young adult females on the Yellowstone suggested they delayed body growth in favor of reproductive success as influenced by a comparatively higher nutritional plane during winter.

Table 6. Sex and age ratios of white-tailed deer on the Elk Island and Intake units during early fall, 1980-86.

	Elk Island			Intake		
Year	N	Fawns: 100 Does	Bucks: 100 Does	N	Fawns: 100 Does	Bucks: 100 Does
1980	253	118:100	37:100	152	115:100	38:100
1981	77	111:100	64:100	164	86:100	27:100
1982	273	111:100	65:100	217	78:100	49:100
1983	112	74:100	50:100	182	67:100	47:100
1984	77	76:100	26:100	120	61:100	49:100
1985	179	106:100	73:100	122	70:100	20:100
1986	136	95:100	53:100	121	68:100	27:100

Whole weights of fawns, estimated from field-dressed weights during autumn were only slightly less than those of late winter/early spring that were determined from heart girth (Table 7). Male fawns were slightly heavier than females from late autumn through early spring.

Females older than fawns maintained their autumn weights through January and experienced slight losses of weight during February and March. Females age classes 1, 2, and 3+ lost 11, 2, and 9% of their respective autumn weights by late winter-early spring. Mean autumn weights of 2-year-old females did not depart appreciably from those of yearlings (Table 7), whereas females 3 years and older were heavier than younger adult females during all seasons.

Among males, whole weight increased progressively with age (Table 7), and this trend was apparent during all seasons. Weight loss from late autumn to early winter was readily apparent among males older than fawns. Weight losses, experienced from late autumn to late winter/early spring were 22, 22, and 30% for males of ages of 1, 2, and 3+ years, respectively.

KFI.--The KFI was characterized (Table 8) by greater variability than whole carcass weights (Table 7), although, as with whole weights, the KFI varied seasonally by sex and age. ANOVA indicated differences ($P < 0.001$) among seasons, age classes, and season/sex interaction, but not between study units and other interactions ($P > 0.10$).

Indexes were highest during autumn and/or winter and lowest during spring and summer coinciding with yearlong maximum and minimum whole weights within age classes older than fawns. Although a decline in the KFI among both sexes of fawns was apparent from winter to spring, seasonal differences were not significant ($P > 0.05$). That fawns mobilized body fat while

Table 7. Estimated whole weights (kg) by season, sex and age of white-tailed deer on the lower Yellowstone River, 1980-86.

Sex and Age Class	Late Autumn	Early Winter	Late Winter/ Early Spring
Females:			
0	33 ± 1(14)[a]	35 ± 1(18)	35 ± 1(13)
1	53 ± 1(18)	49 ± 1(9)	47 ± 3(4)
2	51 ± 2(7)	51 ± 2(7)	50 ± 2(7)
3+	58 ± 1(22)	60 ± 2(7)	53 ± 1(10)
Males:			
0	34 ± 1(13)	38 ± 1(19)	38 ± 2(19)
1	65 ± 1(25)	57 ± 2(4)	51 ± 2(7)
2	76 ± 2(13)	62 ± 5(2)	59 ± 2(10)
3+	87 ± 4(17)	--	61 ± 1(2)

[a] Seasonal mean weight (kg) ± SE (sample size).

Table 8. Mean seasonal kidney fat indexes (KFI) of white-tailed deer by sex and age class from the lower Yellowstone River, 1980-1986.

Sex and Age Class	Summer	Autumn	Winter	Spring
Females:				
0	--	59 ± 9(5)[a]	58 ±15(7)	34 ±11(7)
1	46 ±16(6)	129 ±30(5)	162 ±29(7)	48 ± 9(7)
2+	43 ±17(10)	99 ±14(17)	118 ±17(17)	53 ±10(17)
Males:				
0	--	53 ±13(10)	59 ±22(4)	13 ± 4(4)
1	29 ±11(4)	141 ±28(10)	52 ± 1(2)	30 ± 8(3)
2+	16 (1)	159 ±29(6)	68 ±12(6)	21 ± 1(2)

[a] Seasonal mean ± SE(sample size).

maintaining their weight through early spring, suggested some body growth through winter.

Differences attributable to age, when fawns were excluded from the analysis, were not significant ($P > 0.10$). Thus, yearling and older deer were combined for subsequent analyses. The KFIs of yearling and older males were characterized by increases ($P < 0.05$) from summer to autumn and significant declines from autumn to winter. Those of similar aged females were also characterized by significant increases from summer to autumn. Females apparently continued to accumulate perirenal fat into winter, though differences between autumn and winter were not significant. A decline ($P < 0.05$) in the mean KFI of females was observed from winter to spring.

During autumn, highest mean KFIs occurred among yearling and older males (147%), followed by yearling and older females (106%) and fawns (59 and 53% for females and males, respectively). Differences between adult males and all other groups were significant ($P < 0.05$) as was the difference between adult females and male fawns. Yearling and older females exhibited the highest mean KFIs during winter (130%), followed by yearling and older males (64%) and fawns (58 and 59% for females and males, respectively). Differences between adult (1+) females and all other groups were significant ($P < 0.05$) as was the difference between adult males and female fawns.

KFIs for deer on the lower Yellowstone were comparatively higher than reported for other areas of eastern Montana (Allen 1968, Dusek 1987). The annual cycle by sex and age was generally consistent with that reported by Kie et al. (1983) and Johns et al. (1984). That yearling and older female white-tailed deer on the lower Yellowstone continued to accumulate perirenal fat through winter departed from data reported for mule deer by Anderson et al. (1972) that suggested the KFI generally peaks just prior to or at the peak of breeding.

Diastemal and Main Antler Beam Length.--Diastemal length of yearling males during autumn was correlated with field-dressed carcass weight ($r = 0.49$, 18 d.f, $P < 0.05$). A nonsignificant ($r = 0.21$, 14 d.f., $P > 0.05$) relationship between main antler beam length and carcass weight suggested that factors affecting antler growth differed from those influencing body size. Coefficients of variation between years ranged from 5 to 7% for diastemal length and from 18 to 41% for antler main beam length.

Diastemal length of yearling males during autumn was inversely related to numbers of adult (2+) females during summer and positively related to precipitation during both the immediate preceding September, October, April, and May and the same months of the previous year (preceding birth of the cohort) ($P < 0.01$). These 3 factors accounted for 99% of the variation in diastemal length. The highest and lowest mean diastemal lengths were observed in 1980 and 1984, respectively (Table 9); a decline ($P < 0.05$) was observed from 1983 to 1984.

Table 9. Trends in mean diastemal and main antler beam lengths (mm) of yearling male white-tailed deer on the lower Yellowstone River, 1980-85.

	Year					
	1980	1981	1982	1983	1984	1985
Diastema Length	71 ± 1(18)[a]	71 ± 1(26)	70 ± 1(23)	71 ± 1(15)	66 ± 1(21)	69 ± 1(12)
Main Beam Length	265 ±17(17)	256 ±13(25)	267 ±10(23)	252 ±18(16)	191 ±19(17)	222 ±15(9)

[a] Annual mean measurement (mm) ± SE (sample size).

The negative effects of adult female numbers and the positive effects of precipitation of the immediate past autumn-spring period also appeared to explain 85% of the yearly variation in average main antler beam length ($P = 0.06$). A density-antler growth relationship was also reported for supplementally fed deer (Ozoga and Verme 1982). Average beam length declined ($P < 0.05$) from 1983 to 1984, but years of maximum and minimum average beam length coincided with a year of maximum annual precipitation (1982) and the 2nd of 2 consecutive years of below normal precipitation (1984), respectively. Yearling males with antlers consisting of single tines or "spikes" accounted for 20, 17, 24, 50, 50, and 54% during the respective years, 1980 through 1985. The influence of precipitation only during the immediate past autumn-spring suggested that antler growth was more sensitive than diastemal length to yearly variation in environmental conditions. The lower jaw is a zone of priority growth (Reimers 1972).

The cumulative influence of precipitation received in successive years appeared to have a more profound influence on body growth than on antler growth. This was indicated by less variation in diastemal length between years and a positive correlation between diastemal length and dressed carcass weight of yearling males. Interaction of population size and precipitation may have affected growth of yearling females similarly, though diastemae of young females were not measured during this study.

Seasonal precipitation has been cited as a key variable affecting annual rangeland forage production, although the precise relationship may vary with geographical location, plant species, and other interacting environmentral variables (Blaisdell 1958, Shiflet and Dietz 1974). Precipitation over consecutive years may have cumulative effects on forage production (Hanson et al. 1982, Wisiol 1984). Precipitation for the combined months of September, October, April, and May was most highly correlated with antler or diastemal length measured the following autumn, but coefficients were not significant ($P > 0.05$). Precipitation during those months presumably influenced the availability and abundance of natural herbaceous forage during the early growing season, a period when this type of forage was used most heavily by deer.

REPRODUCTION

Breeding and Fawning Seasons

Back-dated ages of fetuses from 38 females collected between 21 January and 24 April suggested that breeding occurred between 12 November and 28 December with a median date of 21 November. Thirty (79%) bred between 14 and 28 November. Median breeding dates for mature and yearling females were 20 and 27 November, respectively. The estimated date of breeding for the only fawn

among the sample of pregnant females was 26 November. Assuming a period of gestation of about 200 days (Severinghaus and Cheatum 1956), parturition occurred from early June to mid July with a median date of about 10 June. Although the earliest observation of a newborn fawn with a radio-collared female was 9 June, 1982, fawns were not readily observed until mid-June.

Thirty-six females (95%) presumably bred during their first estrus cycle as interpreted from the clustering of breeding dates during the last 2 weeks of November. Two mature females conceived from mid to late December presumably during a second estrus cycle (Cheatum 1949).

Although the peak of breeding among adult (2+) females varied little between years, that for 1984 (23 Nov.) was a few days later than in 1981 (19 Nov.) and 1983 (15 Nov.). Median breeding dates for all years combined were 22 November in the portion of river bottom above Intake and 19 November below Intake.

The breeding cycle of deer is presumed to reflect photoperiodism and generally progresses from November in northern latitudes to January or February in southern latitudes in the U.S. (Verme and Ullrey 1984). The mid-to-late November peak in breeding on the lower Yellowstone River was similar to that reported for New York (Cheatum and Morton 1946, Jackson and Hesselton 1973), and the Midwest (Roseberry and Klimstra 1970, Haugen 1975).

Pregnancy Rates

Breeding was a rare occurrence among fawns. Only 1 of 56 fawns, for which reproductive status was determined from reproductive tracts (n = 17) during 1980-85 or serum assay (n=39) during 1984-86, was pregnant. This contrasts with findings in the Midwest agricultural region where a high incidence of fawn pregnancy was attributed to availability of high quality forage (Roseberry and Klimstra 1970, Haugen 1975).

Sexual maturity of female fawns has been predicated on the basis of autumn weights (Cheatum and Severinghaus 1950). Female fawns of 6-7 months of age were reported to reach sexual maturity at whole weights of 39-41 kg (Verme and Ullrey 1984) or 31-33 kg (Roseberry and Klimstra 1970). Growth rates, primarily as influenced by energy intake, may influence physiological development (Abler et al. 1976).

Whole weights of female fawns on the lower Yellowstone (Table 7) did not change appreciably from November at a median age of 5 months to December and January at median ages of 6-7 months. By November, 11 of 13 female fawns had reached a weight of 31 kg or greater, and only 1 attained a weight of 39-41 kg. By December-January, 16 of 18 female fawns had reached the threshold of 31 kg, while only 2 weighed more than 39 kg. The

variation in critical weights reported in the literature and the negligible change in weight from autumn to winter among fawns in this study indicated that weight alone is not a sound criteria for attainment of sexual maturity among fawns.

Mueller and Sadlier (1979) indicated that relative physiological state, rather than body size, may be the major determinant of sexual maturity among black-tailed deer (O. h. columbianus). They documented a leveling off of whole weights among fawns from November through winter as found in our study (Table 7). This suggested that at the onset of winter-like conditions from mid-November to early December, attainment of sexual maturity may be sacrificed in favor of redirection of resources to growth and maintenance. Suppression of the final stages of puberty and ovulation in white-tailed deer fawns in northern Michigan was attributed to the combined effects of photoperiod and winter-like weather acting on the neurohormonal regulatory mechanisms of puberty (Budde 1983). Because of latitude and prevailing environmental factors in the northern Great Plains, a high incidence of fawn pregnancy probably rarely occurs even in spite of a comparatively high nutritional plane.

The late November breeding date of the single pregnant fawn in the sample suggested that successful breeding among this age class may be limited to either the most precocious or earliest born females. Some adult males began shedding antlers during mid December suggesting a decline in breeding activity (Robinson et al. 1965). However, this does not account for the low incidence of pregnancy among fawns, because of mid-December breeding dates of some older females and observed breeding behavior among males with antlers.

Among 134 yearling and older females examined (60 reproductive tracts and 74 serum samples), 93% were pregnant. Pregnancy rates increased with age through 3-6 years: 32 (86%) of 37 yearling females, 31 (94%) of 33 2-year-old females, 42 (98%) of 43 females of 3-6 years, and 20 (95%) of 21 females 7 years and older were pregnant. However, differences between age classes for all years combined were not significant ($P > 0.10$).

Annual pregnancy rates appeared to vary more among yearling than older females (Table 10). Coefficients of variation between years for yearling and adult females were 16% and 5%, respectively. All 31 yearling and older females examined during winter/early spring of 1981 through 1983 were pregnant (Table 10). Five (19%) of 27 yearlings and 4 (5%) of 76 adults were not pregnant among females examined during 1984-86 when pregnancy rate was dependent ($P < 0.05$) on age.

Table 10. Annual rates of pregnancy (%) of yearling and older female white-tailed deer on the lower Yellowstone River.

Year	Bred[a]	Yearling Females N	Yearling Females % Preg.	Adult Females N	Adult Females % Preg.
1980,	1982	3	100	3	100
1981		7	100	18	100
1983		8	88	19	89
1984		16	81	43	95
1985		3	67	14	100
Total		37	86	97	96

[a] Data were collected during winter or early spring following breeding season.

Reproductive Potential

Potential productivity of the lower Yellowstone population in terms of ovulation and fetal rates, determined from examination of 60 reproductive tracts from yearling and older females during 1980-86 (Table 11), was comparable to that reported for other populations in the northern Great Plains and Rocky Mountains (Table 12). Ovulation and fetal rates were higher than that reported for the southern U.S. but slightly lower than that reported for the Midwestern agricultural and forest regions. The greatest difference between midwestern deer and those from the lower Yellowstone was observed among yearling females. Reproductive performance of the youngest breeding age class has been a classic indicator of overall herd productivity (Ransom 1967, Verme 1969, Mansell 1974).

Ovulation and fetal rates increased with age suggesting that females of 3 to 6 years (4-7 yrs. at parturition) exhibited the greatest reproductive potential (Table 11). The pooled sample of females from all years suggested a potential of 180 fetuses:100 pregnant females and 168 fetuses:100 total females older than fawns. Increasing reproductive potential with age was also reported by others (Roseberry and Klimstra 1970, Mansell 1974, Woolf and Harder 1979).

Fetal rates, like pregnancy rates, varied between years for which comparative data were available: 193:100 total females in 1982 (n = 24), 175:100 in 1984 (n = 13), and 153:100 in 1985 (n = 16). The low rate in 1985 followed 2 years of below normal precipitation (Fig. 2). It also followed the peak in total autumn numbers by one year (Fig. 6).

Table 11. Potential productivity of white-tailed deer on the lower Yellowstone from collection of reproductive tracts during winter and spring, 1980-85.

Age	No. Females	No. Pregnant	Fetuses:100 Preg. Fem.	Fetuses:100 Females	Ovulation[a] Rate
0	17	1	100	6	1.00
1	19	17	141	126	1.41
2	13	12	192	177	1.88
3-6	16	16	213	213	2.28
7 +	12	11	182	167	2.11

[a] Ovulation rates were based on 43 of the 77 total females from which reproductive tracts were examined.

Of 81 corpora lutea of pregnancy from 42 females for which both ovaries were examined, 75 resulted in viable, implanted embryos. The overall fertilization rate (93%) was comparable to that reported for the Midwestern agricultural region (Haugen 1975). Fertilization rates (85-100%) did not differ ($P > 0.10$) between age classes among data pooled for all years. Females in age classes 4, 6, and 7+ had the lowest fertilization rates, 92, 88, and 85%, respectively, but also exhibited the highest ovulation rates (Table 11).

The pregnant fawn carried a single fetus. Among older pregnant females, 7 (41%) of 17 yearlings, 10 (83%) of 12 2-year-olds, 14 (88%) of 16 aged 3-6 years, and 9 (82%) of 11 7 years and older carried twins or triplets. The 4 sets of triplets were all from females 3-6 years of age.

The pooled sample of females for all years indicated that yearlings produced more male than female fetuses (425:100, n = 21, $P < 0.05$). The sex ratio among fetuses of older females (124:100) did not depart ($P > 0.10$, n = 65) from an expected 1:1 ratio. The age-specific trend in fetal sex ratios generally agrees with that reported by Dapson et al. (1979) and others.

Net Productivity

Net productivity, or recruitment, is used here to express the number or proportion of young surviving to autumn or approximately 4 months of age. Overall productivity of white-tailed deer on the lower Yellowstone declined from 1980 to 1984 and increased slightly in 1985. This trend was evident from herd composition and age ratios from autumn aerial surveys (Table 5) and from fawn-at-heel ratios during July through early October (Table 13). Ratios of fawns:100 producing females among pooled samples of females with 1 or more fawn(s) at heel during July-August and September-October for all years were 150:100 (n = 538)

Table 12. Reproductive potential of white-tailed deer across the inhabited range in North America.

Geographical Location	Ovulation Rate		Fetal Rate		Source
	Yrlg.	Ad.	Yrlg.	Ad.	
Southeast					
Florida	--	--	1.14	1.32	Richter and Labisky (1985)
Southwest					
South Texas	--	--	1.32	1.59	Barron and Harwell (1973)
Llano Basin, Texas	1.27	1.56	0.75	1.08	Teer et al. (1965)
Coastal Texas	--	--	--	1.57	White (1973)
Midwest Agr.					
Iowa	2.36	2.23	2.00	2.23	Haugen (1975)
Illinois	1.93	2.24	1.76	1.94	Roseberry and Klimstra (1970)
Regionwide	--	--	1.66	1.91	Gladfelter (1984)
Midwest Oak/Hickory Forest					
Regionwide	--	--	1.66	1.87	Torgerson and Porath (1984)
Northern Great Plains					
L. Yellowstone R.	1.41	2.09	1.26	1.88	This study
Long Pines	--	1.80	--	1.80	Dusek (1980)
Northern Rocky Mts.					
Swan Valley NW MT	1.30	1.95	1.25	1.64	Mundinger (1981)
Idaho	1.50	2.09	1.50	1.88	Will (1973)
Southern Manitoba					
Whiteshell	1.22	1.92	1.00	1.89	
Turtle Mt.	2.00	2.18	1.71	1.87	Ransom (1967)
Duck Mt.	1.43	2.00	1.29	1.92	
Ontario	1.21	1.74	0.82	1.31	Mansell (1974)

Table 13. Productivity of adult white-tailed deer females on the Yellowstone River from the number of fawns-at-heel during July-October 1980-85.[a]

	Fawns:100 Producing Females	% of Ad. Females Producing	% of Producing Females w/		
			Singles	Twins	Triplets
Sept./Oct. 1980	154:100 (133)[b]	68	47	51	2
Jul./Aug. 1981	162:100 (101)	--	41	57	3
Sept./Oct. 1981	154:100 (123)	60	51	43	6
Jul./Aug. 1982	154:100 (96)	--	49	48	3
Sept./Oct. 1982	143:100 (164)	60	58	41	1
Jul./Aug. 1983	152:100 (135)	--	52	44	4
Sept./Oct. 1983	143:100 (95)	49	57	43	--
Jul./Aug. 1984	137:100 (105)	--	64	35	1
Sept./Oct. 1984	127:100 (81)	46	73	27	--
Jul./Aug. 1985	143:100 (101)	--	58	41	1
Sept. 1985	152:100 (27)	42	52	44	4

[a] Sample obtained from Elk Island, Seven Sisters, and Intake study areas.

[b] Sample size of producing females in parentheses.

and 146:100 (n = 623), respectively. These ratios cannot be directly compared with the potential rate per pregnant female (180:100), because they did not account for females that lost all fawns.

The trend in the ratio of fawns:successful females during September and October (Table 13) suggested a decline in reproductive success from 1980 to 1984 and an increase from 1984 to 1985. The proportion of successful females that reared twins or triplets also declined. Of 515 females observed with fawns-at-heel during September-October of all years, 215 (42%) were accompanied by twins and 11 (2%) by triplets.

Age-specific reproductive rates, determined from individually marked females during 1980-86 (Table 14), indicated that reproductive success increased with age to 4 years, declined slightly among 5-year-olds, increased again among 6-7 year-olds, and declined among females 8 years and older. Only 2 (5%) of 44 yearling females successfully reared fawns (1 each during 1980 and 1983). This, together with the low incidence of pregnancy among fawns, indicated that females younger than 2 years did not contribute to reproduction ($P > 0.10$). Of 227 records of reproductive success among marked females older than yearlings, 170 (75%) successfully reared 261 fawns. Expanding these data, on the basis of female age class structure and age-specific fetal and recruitment rates, resulted in a fawn:adult female ratio of 82:100 that compared to a mean of 85:100 from pre-hunt aerial herd composition surveys.

Reproductive status of 57 females 2 years and older during 2 or more successive years provided 95 2-year reproductive histories. Females successfully reared fawns during both years in 58 (61%) cases, reared fawns in alternate years in 24 (25%) cases, and failed to rear fawn(s) during both years in only 13 (18%) cases. Of 36 cases of 3-year reproductive histories among 24 females, 22 (61%) were successful during all 3 years, and 3 (8%) failed in 3 consecutive years. Nine females provided 11 cases of 4-year histories of which 4 successfully reared fawns and none failed during 4 consecutive years. Two females had 5-year histories, and both successfully reared fawns during all 5 years. Of 4 females with 2 or more successive years of reproductive failures, 3 initially failed as 2-year-olds, and 1 was 8 years old. All 4 were from the Intake unit.

Of individually marked adult (2+) females, all of 5 in 1980, 19 (86%) of 22 in 1981, 28 (82%) of 34 in 1982, 32 (78%) of 41 in 1983, 31 (67%) of 46 in 1984, 30 (68%) of 44 in 1985, and 23 (70%) of 33 in 1986 successfully reared fawns. The data from all females observed during September and early October also suggested a decline in the proportion of females successfully rearing fawns from 1980 to 1985 (Table 13). In spite of the fact that yearling females accounted for 34% of all adult females during summer 1980, only 32% of 133 observed females did not successfully rear fawns. This suggested that nearly all females older than yearlings successfully reared fawns that year.

Table 14. Productivity of white-tailed deer on the lower Yellowstone from 155 individually marked females observed during June through October, 1980-86.

Age	No. Females	No. Females Successfully Rearing Fawn(s)	Fawns:100 Producing Females	Fawns:100 Total Females
1	46	2	100	4
2	45	30	137	91
3	48	36	153	115
4	38	31	161	132
5	29	21	152	110
6	23	23	152	152
7	15	14	157	147
8 +	25	15	140	84

Assuming the contribution of yearling females to annual production was negligible during 1981-85, and that 26, 31, 27, 25, and 21% of the females older than fawns were yearlings during the respective years, expanding the data in Table 13 resulted in fawn-rearing success of 86, 91, 76, 71, and 63% for all females older than yearlings during those years. This trend was similar to that among individually marked females during 1980-85. In 149 cases of reproductive success among marked females, 69 (46%) were accompanied by twins and only 1 case was documented of a marked female successfully rearing triplets.

Reproductive success among individually marked females varied inversely with population size, and 2 and 3 year-old females appeared more sensitive to these changes than older females (Fig. 9). A negative linear relationship existed between numbers of adult (2+) females during summer and reproductive success among both 2 and 3 year-old females ($P < 0.01$) and older females ($P < 0.05$). Numbers of yearling females and yearling and older males did not contribute to this relationship ($P > 0.10$). A paired t-test indicated lower ($P = 0.05$) reproductive success among females of 2 and 3 years of age than among older females.

Although net productivity fell short of the potential for the lower Yellowstone population, nearly two-thirds of the females of fawn-rearing age successfully reared fawns in successive years. This was in contrast to northwestern Montana, where net productivity was characterized by alternate year success predicated by physiological stress of winter on females (Mundinger 1981).

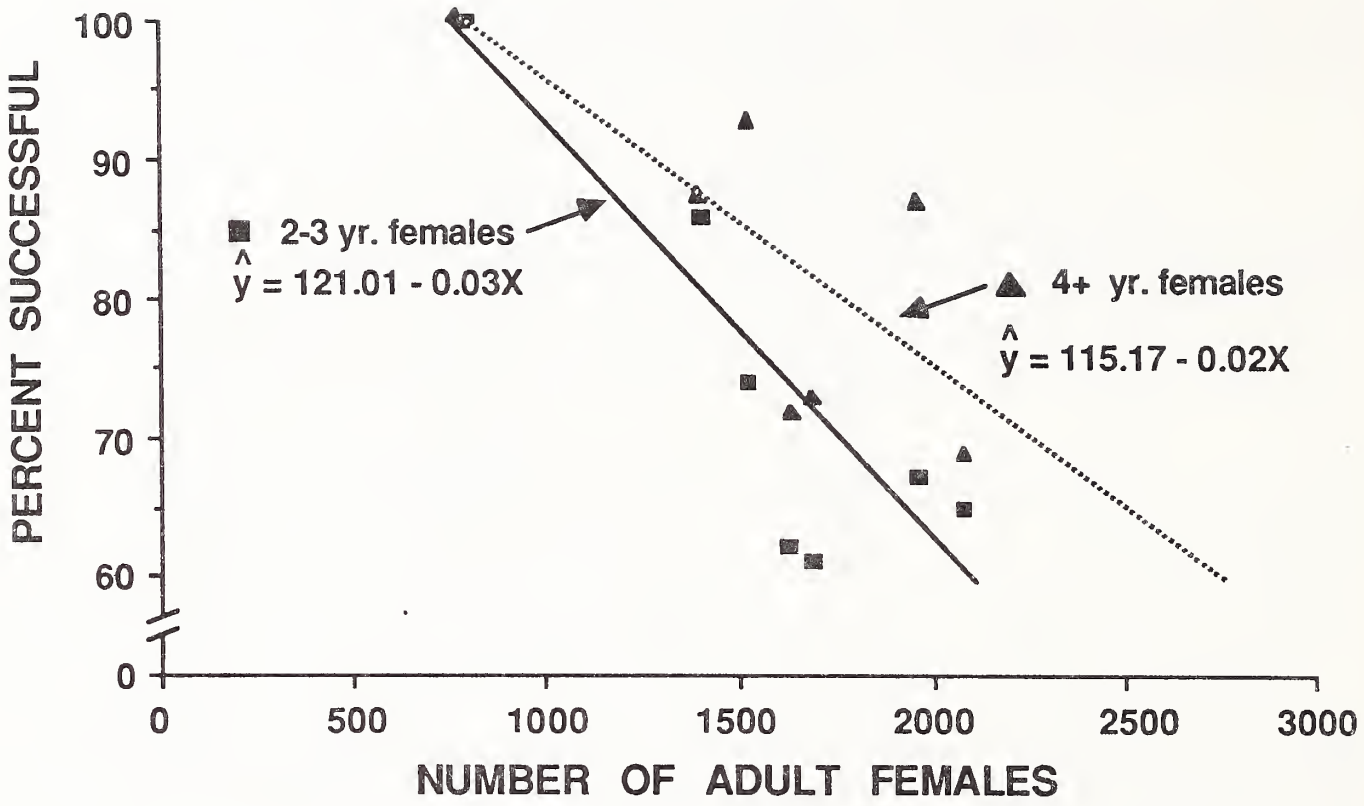


Figure 9. The relationship of summer density of mature females to reproductive success of 2-3 year-old and older females on the lower Yellowstone River, 1980-86.

Spatial Variation in Reproduction and Recruitment

Fawn:adult female ratios (Table 6) and age-specific reproductive rates for marked females (Table 15) suggested that net productivity was lower at Intake than at Elk Island. Age-specific pregnancy and fetal rates were also lower at Intake.

Reproductive patterns of marked females indicated that reproductive success, age of females, and geographic location were mutually dependent (Chi-sq. = 41.503, 7 df, $P < 0.001$). The frequency of reproductive success among young adult (2-3 yrs.) and old (8+ yrs.) females at Intake was less than expected ($P < 0.05$). In contrast the frequency of reproductive failures among prime-age females (4-7 yrs.) at Elk Island was less ($P < 0.05$) than expected. Differences between fetal rates and net productivity indicated that approximately one-half of the reproductive potential of yearling and older females was lost over summer at Intake; at Elk Island, the loss was only one-third of the potential.

Table 15. Spatial variation in potential productivity and recruitment of female white-tailed deer on the lower Yellowstone River, 1980-85.

Age	Above Intake	Below Intake
Pregnancy Rates		
Yrlg.	83% (12)	91% (23)
2+	91% (45)	98% (52)
Fetal Rates		
Yrlg.	100:100 (7)[a]	155:100 (11)
2+	156:100 (16)	200:100 (26)
Fawn-rearing Success		
2	43% (14)	78% (27)
3	44% (16)	92% (25)
4-7	79% (39)	90% (51)
8+	22% (9)	92% (12)
Net Productivity (Fawns:Females)		
2	50:100 (14)	104:100 (27)
3	63:100 (16)	144:100 (25)
4-7	108:100 (39)	149:100 (51)
8+	22:100 (9)	133:100 (12)
% Multiple Births		
2	17% (6)	33% (21)
3	43% (7)	56% (23)
4-7	35% (31)	67% (46)
8+	--	45% (11)

[a] Sample size is in parentheses

MORTALITY

Neonatal/Summer Fawn Mortality

All 101 fetuses from 55 pregnant females examined from the end of the 2nd through the 5th month of gestation appeared viable and normally developed. Because of this, we assumed that the difference between fetal rates and autumn fawn:adult female ratios reflected mortality occurring from parturition through 4 months postpartum. Others studies (eg. Teer et al. 1965) have documented only negligible fetal mortality in deer.

Neonatal and summer fawn mortality was 10, 31, 28, 44, 48, and 33% for the years 1980-85, respectively. There was a positive linear relationship ($P < 0.05$) between summer fawn mortality rates and adult female density (Fig. 10). Numbers of females of 2 years of age and older in summer populations accounted for 98% of the variability in oversummer mortality of

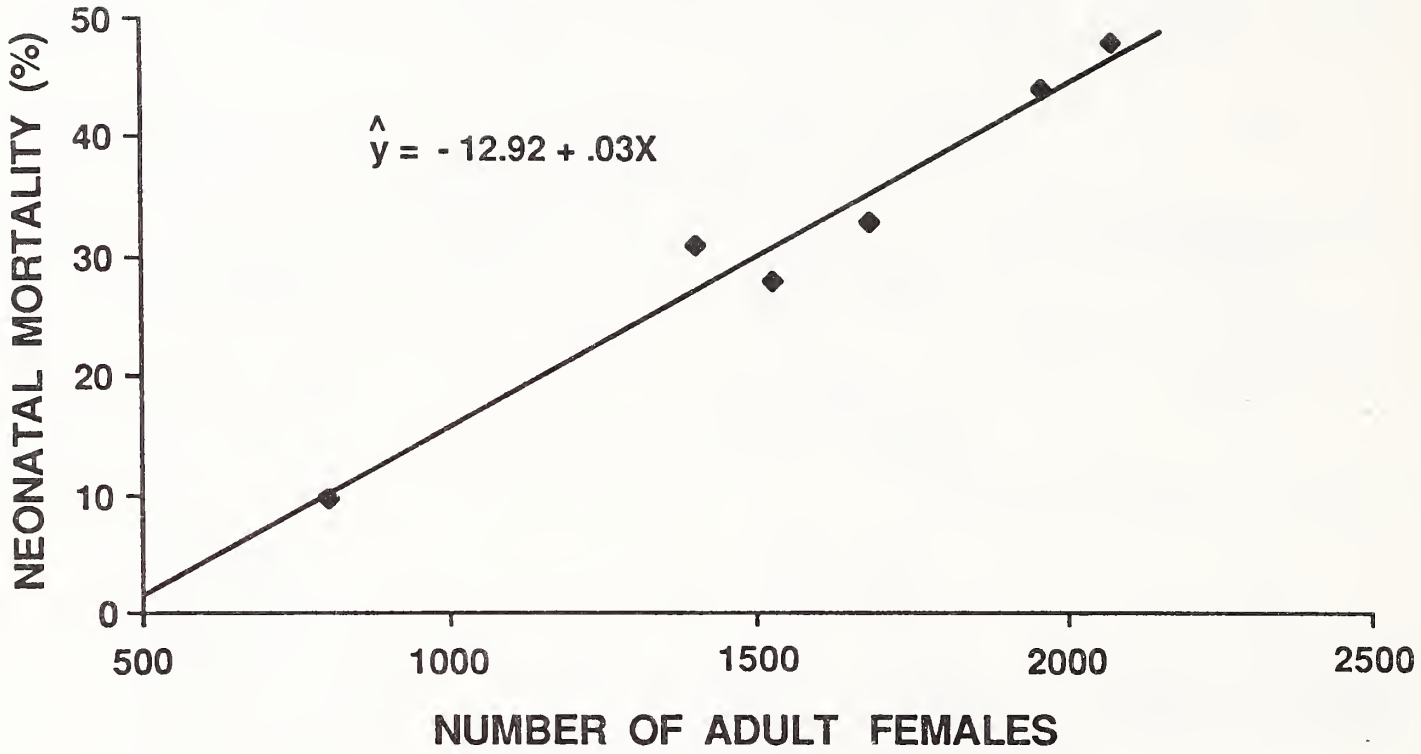


Figure 10. The relationship between summer fawn mortality and density of 2 year-old and older females, 1980-86.

fawns. Densities of yearling females and yearling and older males did not significantly contribute to this relationship.

Fawn mortality appeared to occur largely during the first month of life. Little change was observed in the fawn-at-heel ratios from July/August to September/October (Table 13). Of 48 individually marked females of 2 years of age and older that failed to successfully rear fawns during 1981-85, only 6 were observed with fawns through late July.

Rates of summer fawn mortality on the lower Yellowstone fell within the range reported for the species. Relatively high fawn mortality within 90 days of the peak of fawning was reported by Teer et al. (1965) and Gavin et al. (1984). Cook et al. (1971) and O'Pezio (1978) also reported nearly all summer fawn mortality to occur within one month postpartum.

General Patterns of Mortality

Estimates of annual mortality were 17, 22, 29, 36, 42, and 42% during the biological years ending in May 1981-86, respectively. Average annual mortality of yearling and older males was more than twice that of yearling and older females (Table 16). The average annual rates for individually marked females (31%) and males (59%) were slightly higher than those

Table 16. Annual and seasonal rates of mortality (%) for white-tailed deer on the lower Yellowstone River, 1980-86.

Season	Fawns	Total Adult (1+)	Adult Female	Adult Male
Annual	50 (± 7)[a]	34 (± 4)	22 (± 6)	60 (± 7)
Jun.-Aug.	32 (± 5)	0 (± 1)	0 (± 3)	0 (± 6)
Sep.-Nov.	19 (± 6)	29 (± 4)	18 (± 4)	55 (± 7)
Dec.-May	10 (± 2)	6 (± 2)	5 (± 2)	6 (± 2)

[a] Percent mortality (± SE)

determined from seasonal population estimates but still emphasized the higher rate among males than females.

Mortality among deer older than 4 months, as determined from population estimates (Table 16), was highest during autumn and lowest during summer. Nearly all adult mortality (88%) occurred during autumn. The average fawn mortality rate from September through May was 26%, and similar to adults, most deaths (67%) occurred during autumn. Of 179 confirmed deaths of marked deer (Table 17), 154 (86%) died from September through November, 13 (7%) died during winter, 9 (5%) during spring, and 3 (2%) during summer.

An increase in annual mortality rates from 1980-81 to 1984-85 reflected increases in hunting-related mortality (Table 18). Hunting accounted for an average of 81% of annual mortality of individually marked deer. Mortality from other causes varied slightly, but was generally low, claiming 5, 9, 5, 6, 11, and 9% of autumn populations during the 6 years, respectively. Among deaths of yearling and older deer during autumn, 5 resulted from accidents and 3 from other or undetermined causes. Only 25 deaths of marked deer were documented during winter, spring, and summer. Three resulted from injury or stress induced by capture and handling, accidents accounted for 7, 3 were related to hunting, 2 were confirmed overwinter mortalities, 1 was a predator kill, and 9 were from undetermined causes.

Hunting Mortality.--In Montana, killing of deer was first restricted by season length in 1872, by bag limit in 1907, and by buck-only hunting in 1921 (Mussehl and Howell 1971). Hunting of white-tailed deer was discontinued in eastern Montana during the early 1940's because of their relative scarcity. As deer numbers increased statewide during the late 1940's and early 1950's buck-only harvest regulations were replaced by one deer, either sex seasons from 1952 to 1954 (Cole 1959). From 1955 to 1957, these were replaced with 2 deer, either sex seasons. From 1960 to 1975, harvest regulations included 2-deer bag limits in southeastern Montana that encouraged the harvest of white-tailed deer in hunting districts where they were the predominant species

Table 17. Number of marked yearling and older white-tailed deer dying from various causes by season and age class, 1980-1986. Causes: A=accidents, H=hunting related, P=predation, T=trap-related, W=winter malnutrition, M=other known causes, and U=undetermined causes.

Female Deaths						
			Season			
Age Class	Number at Start	Total Deaths	Summer	Autumn	Winter	Spring
1	82	19	2A	15H	2U	
2	65	19	1U	14H	1A,1H,1T 1U	
3-7	200	56		43H,2A,2M, 1U	2H,1A,2U	1A,1P, 1U
8+	29	8		4H,1A	1U	1W,1U
Total	376	102	3	82	12	5

Male Deaths						
			Season			
Age Class	Number at Start	Total Deaths	Summer	Autumn	Winter	Spring
1	97	31		2A,27H		2A
2	54	31		29H	1T	1T
3-7	28	15		14H		1W
Total	179	77	0	72	1	4

or where it was desirable to reduce hunting pressure on mule deer (C. D. Eustace and J. E. Swenson. 1977. Montana Dep. Fish, Wildl. and Parks, Fed. Aid Proj. W-130-R, Unpubl. rep.). Restricting one or both tags to white-tailed deer was necessary to increase annual harvests in some areas.

In 1976, following a widespread decline in mule deer populations, hunters were limited to either 1 antlered mule deer or a whitetail of either sex. Increased populations of both species during the late 1970's and early 1980's were followed by increasingly liberalized harvest regulations. The "A" tag allowed taking a deer of either species/either sex, whereas the "B" tag was largely limited to antlerless deer. Multiple "B" tags were offered from 1984 to 1985. In 1984, a hunter could legally harvest 6 white-tailed deer from the lower Yellowstone of which only one could be an antlered deer.

Table 18. Hunting efficiency on the lower Yellowstone River by sex and age class of deer from population and harvest statistics, hunting mortality of marked adult deer, and change-in-ratio procedures.

	Percent Removal by Sex and Age Class				
Year	Total[a] Population	Fawns[b]	Total Adults N=3[d]	Adult[c] Females 1.5+	Adult Males 1.5+ N=3
1980	13	3	21	11	38
1981	14	5	21	6	60
1982	25	10	34	14	68
1983	32	14	40	26	69
1984	35	17	36	30	53
1985	34	22	41	33	57

[a] Calculated from percentage of adults removed with the proportion of fawns and adults in fall populations and annual harvests known.

[b] Calculated with the same knowns given above.

[c] Calculated from the percentage of total adults and males removed with the proportion of adult males and females in fall populations and annual harvests known.

[d] N = the number of independent estimates which give the mean total adults and adult males removed per year.

Hunting-related deaths documented during this study included both legal harvest and deaths resulting from crippling. Some deaths attributed to crippling may have resulted from hunters failing to retrieve their kills or deliberate abandonment, but they were not differentiated.

Crippling losses accounted for 20% of all hunting-related deaths of marked deer, or 24% of the legal harvest, from 1980 to 1985. Archery hunting accounted for 10 (7%) of 148 hunting-related deaths. Two of the 10 died as a result of crippling.

Hunting mortality generally reflected disproportionately heavy harvest of antlered over antlerless deer. Harvest of adult males (2+ yrs.) over represented ($P < 0.05$) their abundance in early autumn populations during all years (Table 19). Yearling males were harvested in greater proportion than their abundance ($P < 0.05$) only during 1980 and 1981. The decline in the proportion of yearling males in annual harvests from 1982 to 1985

Table 19. Composition of annual harvests of white-tailed deer from the lower Yellowstone River from deer examined at check stations and in the field during 1980-85.

	Percent of Total Harvest					
Year	Fwn Male	Fwn Fem	Yr Male	Yr Fem	Ad Male	Ad Fem
1980	4 -[a]	7 -	30 +	12	22 +	25
1981	7 -	6 -	28 +	5 -	38 +	15 -
1982	8 -	7 -	18	10	37 +	20
1983	5 -	9	14	9	26 +	37
1984	12	17	14	10	18 +	28 -
1985	13	11	13	8	22 +	32

[a] A (+) indicates that a sex and age class was harvested in greater proportion ($P < 0.05$) than its representation in the population; a (-) indicates a harvest less than availability ($P < 0.05$); and blanks indicate no difference.

coincided with a significant decline in antler main beam lengths from 1983 to 1984 (Table 9) and liberalized harvest regulations for antlerless deer during 1983-85. The number of hunters reporting difficulty in distinguishing yearling males from antlerless deer was particularly noticeable during 1984 and 1985. The decline in the proportion of all antlered deer in annual harvests from 1981 (66%) to 1984 (32%) (Table 19) also coincided with liberalized regulations and increasing proportions of autumn populations being harvested (Table 18).

The proportion of fawns in annual harvests under represented ($P < 0.05$) their abundance in early autumn populations during all years except 1984 and 1985 (Table 18). This reflected decreased hunter selection against fawns when multiple antlerless tags were available. The proportion of yearling and older females in annual harvests never exceeded ($P > 0.05$) their availability (Table 18). However, yearling females were under represented ($P < 0.05$) in the 1981 harvest and adult females were under represented in 1981 and 1984.

The sex ratio of fawns in samples of hunter-harvested deer did not depart from 50:50 ($P > 0.05$) during any year. Although males consistently outnumbered females among yearling deer in annual harvests, the ratio departed from the expected 50:50 ($P < 0.05$) only during 1980 and 1981.

Harvest of antlered deer was correlated ($r = 0.98$, $P < 0.001$) with their abundance in early autumn populations from 1980 to 1985. This relationship was more difficult to ascertain for antlerless deer because season structure, bag limits, and season length changed from year to year. The increased proportion of

antlerless deer in annual harvests (Table 19) from 1982 to 1983 coincided with increasingly liberalized antlerless regulations.

Others have also indicated that vulnerability to hunting was dependent upon the sex and age of deer. Roseberry and Klimstra (1974) and Coe et al. (1980) reported a tendency of hunters to take adult deer over fawns. The latter study indicated that adult females were most vulnerable among antlerless deer because they were often the first deer seen, and fawns were less vulnerable when in groups than when alone. Roseberry and Klimstra (1974) suggested that yearling and 2-year-old males were harvested at a higher rate than other sex or age classes. They also reported a decline in vulnerability with cumulative hunting pressure from increased wariness as a result of harassment. In the absence of selectivity, adult males may be less vulnerable to hunting than adult females and fawns (Van Etten et al. 1965).

The rate of crippling on the lower Yellowstone was comparable to that reported for the Midwest by Roseberry et al. (1969) and Stormer et al. (1979) but somewhat higher than reported in Texas by Teer et al. (1965). Stormer et al. (1979) attributed a decline in the rate of crippling to a decline in deer density and hunter success. We were not able to detect changes in rates of crippling with changes in population size.

Traffic-related Mortality.--Automobile-deer collisions claimed an average of 2% of autumn populations annually. They accounted for 11 (6%) confirmed mortalities of individually marked deer. Mortality determined from marked deer may have overestimated highway mortality because marked deer dying along roads may have been reported in greater proportion than those dying from natural causes.

The distribution of road-killed deer was nonrandom ($P < 0.001$) in both time and space. Of 170 carcasses examined along roads from 1980 to 1986, 147 (85%) died during October-April (Table 20). October-December and March were peak periods of highway-related deaths when 49% and 15% of this mortality occurred. Most vehicle-deer collisions presumably occurred during crepuscular and nocturnal periods, because many fresh road-kills were first sighted during these periods or shortly after daylight. This also closely agreed with daily periods of maximum activity and movement reported by Herriges (1986).

Over the study, 157 (92%) deer were killed along Highway 16; the remainder died on secondary Highway 23 and on county roads. Seventy-two percent of the kills along Highway 16 occurred within approximately 16% of the distance from Glendive to Sidney; no kills were observed on 20% of that distance.

Topography, distance from the river, and land use did not influence the number of deer killed ($P > 0.10$) per segment (1.6 km) of highway, although there was a tendency for more accidents to occur near the river where agricultural crops were present ($P = 0.12$). Approximately 43% of the highway mortality occurred

Table 20. Monthly auto-related mortality of white-tailed deer along the lower Yellowstone River from April 1980 to May 1986.

	Females			Males			
Month	Fawn	Yrlg.	Adult	Fawn	Yrlg.	Adult	Total
June	--	1	--	--	--	1	2
July	1	3	--	--	1	1	6
August	--	1	1	--	--	--	2
September	--	3	4	3	2	--	13[a]
October	7	3	11	4	1	2	28
November	9	5	6	8	8	--	36
December	4	2	7	4	2	1	20
January	4	2	3	3	--	--	12
February	3	--	3	2	3	--	11
March	3	4	5	5	8	1	26
April	--	2	6	2	--	1	11
May	1	--	--	--	2	--	3
Total	32	26	46	31	27	7	170

[a] Total includes fawn of unknown sex.

less than 2 km from the river channel in areas where agricultual crops were grown (30% of the total distance). The lowest mortality (2% of the total) occured near housing developments or other commercial buildings on the floodplain at distances exceeding 2 km from the river (8% of the total distance).

Composition of highway mortality by sex and age during June-November reflected herd composition of early autumn. Relative numbers of deer killed by sex and age class did not depart ($P > 0.05$) from expected frequencies, nor did sex ratios of fawns and yearlings depart from 50:50. For December-May, the composition of road-killed deer was compared with early winter herd composition. Yearling males were killed in greater proportion than their abundance ($P < 0.05$) in the winter population while mortality of other sex and age classes did not depart from expected frequencies ($P < 0.05$).

Several studies have suggested that trends in traffic mortality reflected gross changes in population size (Jahn 1959, Case 1978). McCaffery (1973) reported that traffic-related mortality most accurately reflected these changes when corrected for changes in traffic volume. Numbers of road-kills examined along the lower Yellowstone per year was not correlated with changes in population size ($r = 0.25$, 4 d.f. $P > 0.10$). This may have reflected unequal rates of recovery between years as well as a change in traffic volume over time.

The aggregated distribution of traffic-related mortality in time and space generally agrees with findings reported by Bellis and Graves (1971), Puglisi et al. (1974), and Bashore et al. (1985). Allen and McCullough (1976) attributed a relatively random spatial distribution of road-kills to similar habitat conditions in an agricultural region of southern Michigan. However, they reported that most car-deer collisions occurred during crepuscular and nocturnal periods. The nonrandom pattern of mortality on the lower Yellowstone in both time and space probably reflected distribution of agricultural fields and daily patterns of activity associated with their use (Herriges 1986).

Movement of individually marked deer into areas they did not routinely use except during periods of comparatively heavy hunting resulted in traffic-related deaths of 3 animals in the Intake unit during late October-early November 1984. Deer moving to feed in winter wheat fields in upland terraces west of Highway 16 during March and comparatively early green-up of roadside vegetation during March and early April may have contributed to the high frequency of highway-related mortality during the early spring period.

Natural Mortality.--Natural mortality claimed an average of 5% of autumn populations during the study. Deaths related to malnutrition during late winter and spring accounted for 3% of confirmed mortalities of individually marked deer for all years combined. All occurred during February-April; 3 of 6 were fawns, 2 were females of 9 years and older, and one was a 4 year-old male. Winter severity and estimates of overwinter mortality of fawns were not correlated ($r = 0.67$, 4 d.f., $P > 0.10$), although highest estimated fawn mortality (17%) occurred during the severest winter, 1981-82 (Table 2). The relatively low incidence of overwinter mortality is consistent with the comparatively good condition in which animals enter the winter period as reflected by the KFI (Table 8). Substantial overwinter mortality was documented during severe winters in conifer habitat in southeastern Montana where deer were in relatively poorer condition than those on the lower Yellowstone (Dusek 1987).

Predation, accidents (not human-related), and undetermined causes collectively accounted for 9% of all confirmed deaths of marked deer. Two marked deer were suspected victims of EHD during late summer 1984, and several sightings or reports of dead deer along the river bottom were obtained. One radio-collared deer died during the same period in 1985. There was one confirmed report of a white-tailed deer with symptoms of hemorrhagic disease from elsewhere in eastern Montana in 1984.

DISTRIBUTION

White-tailed deer occurred throughout the entire length of river bottom, though densities varied. The occurrence of small numbers of whitetails in adjacent uplands and along ephemeral tributary streams appeared to reflect seasonal shifts of some individuals off the river and/or local distribution, movement, and habitat selection relative to specific habitat characteristics.

Diurnal distribution of deer during summer generally centered on large blocks of riparian tree and shrub cover, but also included small, isolated patches of trees and/or shrubs along drainage ditches, the USBR main canal, and field borders. Telemetry and spotlight surveys (Herriges 1986, Compton 1986a) indicated that nocturnal distribution also included agricultural fields. Use of uplands, which included wooded draws, was most prevalent in the Intake area, where the river bottom was narrow and upland riparian cover occurred in close proximity to the river bottom.

Diurnally in winter, deer were distributed almost exclusively in large stands of riparian cover near the main river channel and on some of the larger islands. The only notable exception occurred at Intake during 1983-84 when, coincident with high deer densities, some individuals used upland draws. At Elk Island, many radio-collared deer that summered locally throughout the floodplain shifted their daytime distribution to the large island in winter when ice provided easy access across the river channel. Nighttime distribution in winter extended from the riparian cover used during daytime to agricultural fields throughout the river bottom and, locally, to adjacent uplands. As during summer, use of agricultural fields in uplands was most prevalent on the Intake area.

Habitat Factors Influencing Distribution

Riparian cover, which included shrub and forest cover types, was the single most important factor affecting density distribution of deer within the study area (Fig. 11). A linear relationship ($P < 0.0001$) existed between the amount of riparian cover and numbers of deer observed in 1.6 km segments of river bottom during early winter surveys each year from 1981 to 1985 and for all years combined (Table 21). This factor alone explained 74% of the overall variation in relative abundance of deer observed along the river bottom from the pooled data for all years. These findings generally agree with those of Compton et al. (1988) for a portion of the study area during winter, summer, and autumn of 1985.

The amount of island area may also have influenced distributional patterns. Multiple regression models indicated that island area combined with the amount of riparian cover influenced distribution and relative density of deer ($P < 0.05$)

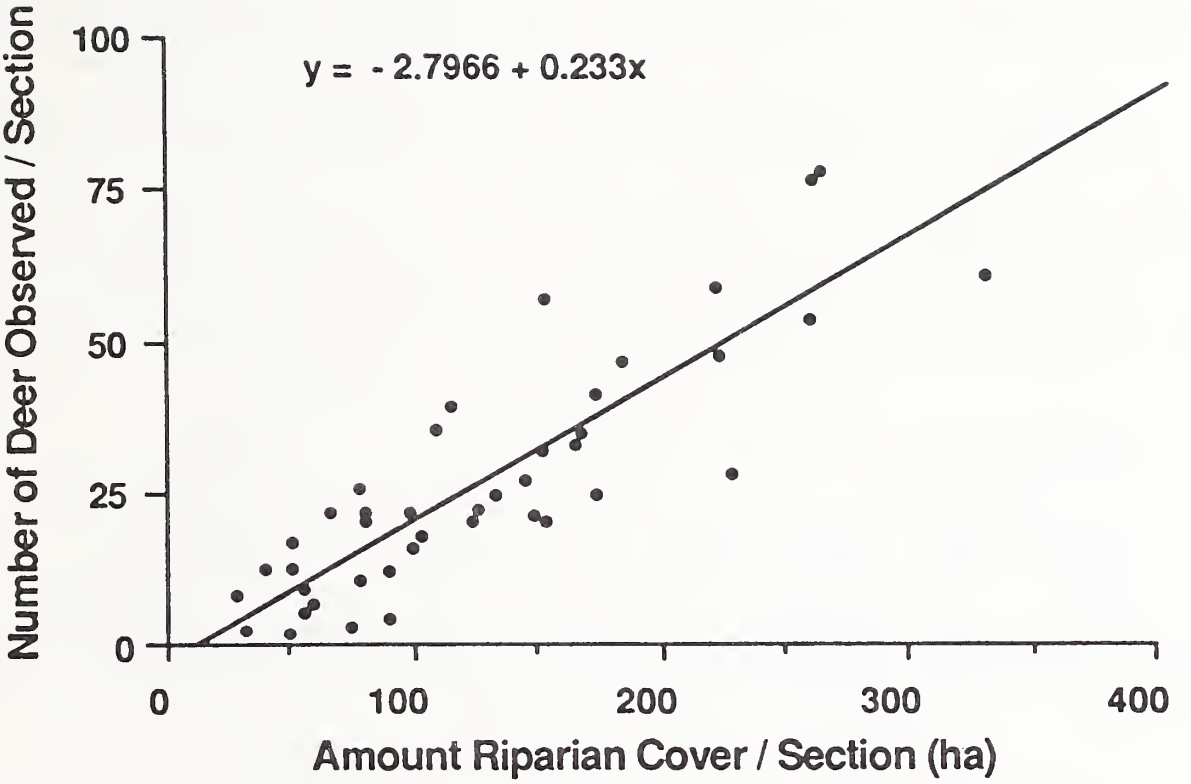


Figure 11. Relationship between abundance of riparian forest/shrub cover (ha) and numbers of deer observed per 1.6 km segments of river bottom during early winter surveys, 1981-82 through 1985-86.

Table 21. Multiple regression models of deer density (Den) per segment of river bottom (dependent) as influenced by the amount of riparian cover (RC) and island area from early winter aerial surveys of the entire lower Yellowstone study area, 1981-82 to 1985-86.

Year	Regression Model	P - value	R^2
1981-82	Den = 2.63 + 0.28RC	< 0.0001	0.49
1982-83	Den = -11.99 + 0.31RC	< 0.0001	0.68
1983-84	Den = 1.27 + 0.29RC	< 0.0001	0.56
1984-85	Den = -2.55 + 0.18RC	< 0.0001	0.55
1985-86	Den = -3.92 + 0.07RC + 0.12IA	< 0.02	0.44
All Years	Den = -3.56 + 0.21RC + 0.06IA	< 0.05	0.77

over all years as well as during winter 1985-86.

Aerial surveys of the Elk Island area indicated increased deer use of the large island from early autumn ($\bar{X}$ = 22%) to a yearlong high during winter ($\bar{X}$ = 40%) and decreased use during spring ($\bar{X}$ = 31%). This pattern was also observed among radioed deer which made minimal use of the island during summer and maximum use during late autumn and winter. In contrast, some deer at Intake used a large island during autumn-spring of all years, but individually marked deer rarely were found there except during the autumn hunting season. The amount of island area was also directly related to density distribution of deer along the river bottom during autumn 1985 (Compton et al. 1988).

Sloughs occurred in 4% of 858 9-ha cells covering the 3 principal study units. Nine percent of 4,932 relocations of marked deer occurred in cells with sloughs, indicating selection ($P < 0.01$) for such areas. Sex and age classes responded differently to the presence of sloughs ($P < 0.01$). Thirteen percent of all (2,476) relocations of mature (+3) females occurred in habitat with sloughs; they were 2.5 times more likely to be found in such areas than other deer.

Influence of Livestock

Studies by Compton et al. (1988) indicated that livestock grazing had a negative effect on local distribution and density of deer along the river bottom. In general, deer avoided areas where cattle were present. Data concerning deer-livestock relationships on the intensive Elk Island and Intake study units, which received markedly different livestock usage, were more specific.

During 1980-86, approximately 70% of the Elk Island area was not grazed, 21% was grazed by cattle from autumn through early spring, and 9% was grazed by sheep from summer through early winter. Under this regime, deer distribution was dependent ($P < 0.01$) upon grazing treatment. During all seasons, marked deer selected ($P < 0.05$) areas that were not grazed and avoided ($P < 0.05$) areas grazed by cattle (Table 22). During summer and winter, deer avoided pastures traditionally grazed by sheep, but use of those pastures by deer did not depart from availability ($P > 0.05$) during autumn and spring.

Seasonal differences in responses of deer to grazing treatment were highly significant ($P < 0.01$). The relative use of nongrazed areas by deer was higher during summer than during all other seasons (Table 22). Sheep pastures received their greatest yearlong use by deer from autumn through spring, whereas relative use of portions of the floodplain grazed by cattle did not appreciably change between seasons.

Table 22. Response of white-tailed deer to nongrazed areas (N), areas grazed by cattle (C), and areas grazed by sheep (S) on the Elk Island area from 2273 relocations of individually marked deer, 1980-86.

Sex and Age Class	Yearlong			Summer			Autumn			Winter			Spring		
	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S
All Deer	V (2273)[a]			V (659)			V (524)			V (561)			V (529)		
	91+	2-	7-[b]	95+	1-	4-	90+	2-	8	90+	4-	6-	89+	2-	9
Ad. Fem.	V (1249)			V (359)			V (311)			V (313)			V (266)		
	95+	1-	4-	96+	1-	3-	95+	2-	3-	96+	1-	4-	94+	1-	5-
Subad. Fem.	V (632)			V (158)			V (124)			V (172)			V (178)		
	88+	3-	9	96+	0-	4-	86+	2-	12	84+	8-	8	84+	2-	14
Ad. Male	V (171)			V (75)			V (52)			(22)			(22)		
	84+	4-	12	95+	5-	0-	69	2-	29+	82	5	14	86	5	9
Yrl. Male	V (221)			V (67)			V (37)			(54)			(63)		
	84+	5-	11	88+	0-	12	86+	0-	14	80	7	13	81	11	8

[a] V - Differences between observed and expected use of grazing treatments by deer in appropriate group and season resulted in significant ($P < 0.01$) chi-sq. values (sample size).

[b] Percent of annual or seasonal relocations in the 3 grazing treatments. Bonferroni Z tests were used to determine which treatments were selected (+) or avoided (-) ($P < 0.05$).

The yearlong influence of grazing treatment on distribution of deer was dependent ($P < 0.01$) on sex and/or age. Both subadult and mature females selected ($P < 0.05$) nongrazed portions of the Elk Island area. Mature (3+) females avoided ($P < 0.05$) areas grazed by both cattle and sheep during all seasons. Yearling and 2-year-old females also avoided areas used by cattle during all seasons but avoided areas grazed by sheep only during summer (Table 22).

Males exhibited no selection or avoidance of habitats with respect to grazing treatment during winter and spring. During summer and autumn, both yearling and older males avoided areas that were traditionally grazed by cattle from autumn to early spring. In summer, adult (2+) males avoided pastures grazed by sheep; in autumn, those areas were selected (Table 22). This may have been largely influenced by hunting pressure; sheep pastures were on privately-owned lands where hunting pressure was much lower than on the adjoining EIWMA and large island. Yearling

males selected ($P < 0.05$) nongrazed areas, but their use of areas grazed by sheep did not depart from availability ($P > 0.05$) during either summer or autumn.

The differential response of sex and age classes to grazing treatment was most apparent during autumn, winter, and spring when the area was most intensively used by livestock, particularly cattle. During autumn and winter, mature (3+) females were 4 times more likely than other deer to occur in nongrazed areas; in spring this probability was 3X. They were 7 times more likely than subadult females or males to occur in areas not grazed by sheep during autumn.

In contrast to Elk Island, nearly all of the Intake area was grazed by cattle from mid autumn through winter (Table 3). There were no apparent differences in deer distribution from spring through mid autumn that could be directly related to winter grazing. Similarly, because of the extensive occurrence of cattle from mid autumn through winter, we were unable to detect any measureable changes in distribution of deer along the river bottom during that period. However, deer use of adjacent, ungrazed uplands for feeding increased after cattle were placed on the bottom during all years. Some used upland areas throughout the diel period during winter 1983-84, when deer densities were highest and cattle were fed on the bottom through most of the winter. Lacking ungrazed areas to which they could move, deer that remained on bottomlands during winter apparently accomodated the presence of cattle through more subtle movements and changes in habitat use.

MOVEMENTS

White-tailed deer on the lower Yellowstone River were generally nonmigratory. Seasonal ranges overlapped among 27 (79%) of 34 radioed adults and 13 (68%) of 19 yearlings. Mean distances between summer and winter geographic centers of activity (GACs) for deer with overlapping seasonal ranges were less ($P < 0.05$) than for those with discrete seasonal ranges (Table 23). Of 13 deer (7 adults, 6 yearlings) with discrete seasonal ranges, yearlong movements of 10 were confined to the main Yellowstone Valley which included the floodplain, islands, adjacent terraces, alluvial plains, and lower reaches of ephemeral streams. Discrete seasonal ranges of 2 yearlings were related to dispersal behavior; as adults seasonal ranges of each animal overlapped.

Of 52 radioed deer monitored for at least one biological year, 49 (94%) had home ranges entirely within the river valley; 3 left the main drainage for periods of 6-7 months during the year. The latter included one female which, as a 3-year-old, spent summer and autumn in upland prairie habitat 9.1 km from her winter home range, but subsequently established a permanent home range on the river bottom approximately 1.5 km from the winter range. A yearling male left the river bottom during June, spent

Table 23. Distance between summer and winter GAC's by sex, age, and seasonal ranges based on analysis of 78 deer years of data from 1980-85.

Type of Seasonal Ranges	Sex and Age	Distance Between GACs (km) N	$\bar{X}$	SE
Overlapping				
	Females			
	Yrlgs.	11	0.40	0.09
	Ads.	44	0.34	0.04
	Males			
	Yrlgs.	2	1.20	0.90
	Ads.	6	0.93	0.20
Discrete				
	Females			
	Yrlgs.	3	6.80	3.80
	Ads.	9	2.87	0.88
	Males			
	Yrlgs.	3	8.73	3.73

the summer and autumn in prairie habitat 14.6 km from his ancestral home range, and returned to the bottom during December. He repeated this movement pattern the following year until killed in November. Another male, a 2-year-old, moved to uplands approximately 12.1 km from the river bottom during July, returned to the bottom in January, and remained there until killed the following November. Other movements by marked deer into uplands were related to daily movement, were of short duration (2 wks. or less), or were dispersals. Fidelity of whitetails to bottomland habitats, with little or only occasional use of uplands, was also reported elsewhere in eastern Montana (Allen 1968), Missouri (Zwank et al. 1979), and Washington (Gavin et al. 1984).

Diurnal Movements

Movement patterns of deer varied ($P < 0.05$) by month, sex and age (Fig. 12). There were no differences ($P > 0.10$) in diurnal movements related to study unit, either alone or in combination with the 3 independent variables.

Movements of deer while in uplands (2% of the total animal months) were not included in the analysis. Monthly AARs of an adult female that spent late spring-autumn in upland prairie habitat (1.70, 0.30, 0.50, and 2.20 km during May, June, July, and September, respectively) were much larger than those recorded

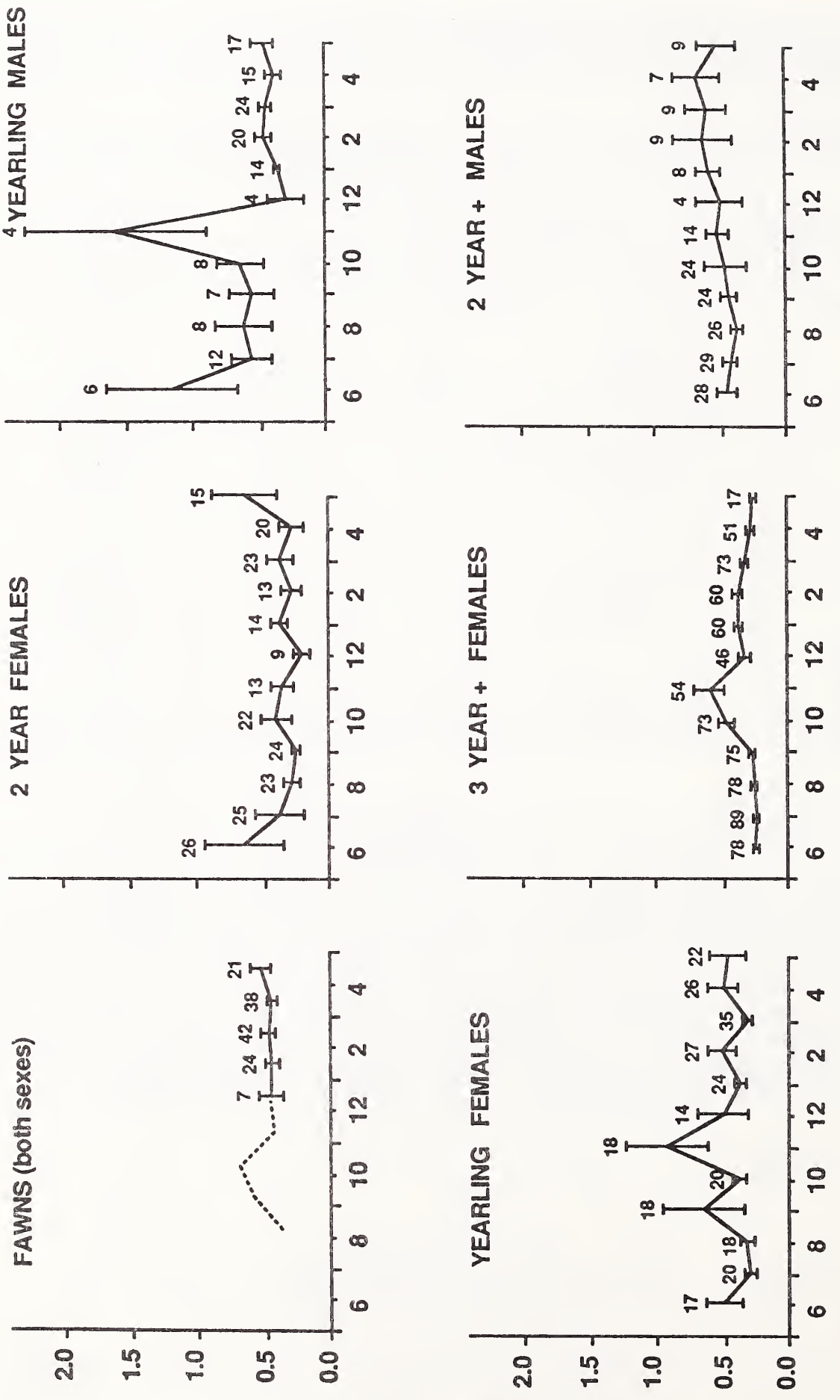


Figure 12. Mean monthly average activity radius (AAR) by sex and age for white-tailed deer on the lower Yellowstone River, 1980-85. Vertical lines represent 2 standard errors.

for females of all ages on the river bottom. The movements of two males, while in uplands, were also generally greater than those of males of the same ages on the bottom. These movement patterns closely fit those reported for whitetails in prairie habitat (Wood 1987), where monthly movement indexes for females were nearly 3 times greater than on the lower Yellowstone.

Monthly movements of fawns on the river bottom during September-December were assumed to approximate those of females of fawn-rearing age. Movements of fawns marked in winter corresponded to those of adult females (3+) from January through April (Fig. 12). The increased movement during May was attributed to the breakup of family groups. Among 4 family groups in which both doe and offspring were radio-collared, the pairs separated between 13 May and 7 July. All offspring (2 females and 2 males) left their ancestral home range, although one female later rejoined its mother.

Comparatively high movement indexes among yearling and 2-year-old females during May and June (Fig. 12) also reflected breakup of family groups and included dispersal of some females from ancestral home ranges. This was consistent with the hypothesized socially subordinate status of these age classes (Hawkins and Klimstra 1970) and was similar to movement patterns reported by Downing and McGinnes (1975).

Ozoga and Verme (1982) and Nelson and Mech (1984) indicated that females may remain with their mothers until about 3 years of age, when some may establish a new home range some distance from the ancestral home range. This could explain the increased movement during May of females nearing their third birthday (Fig. 12). Movement of a radio-collared female from the river bottom just prior to her third birthday may have reflected such movement, but she apparently did not establish a traditional home range until 4 years old. During June, one radio-collared 2 year-old female left the river bottom permanently, another temporarily left her summer home range. Monthly AARs of yearling and 2-year-old females during October-April, although erratic and variable between individual animals, resembled those of older females.

AARs for females 3 years and older were generally less variable between months and between individuals than those of other deer (Fig. 12). They were lowest from May to August, the late gestation and fawning period. Movements increased slightly in September, coincident with weaning of fawns or regrouping of maternally-related females.

The marked increase in the AAR among adult females during October-November coincided with the hunting and breeding seasons. Females commonly responded to hunting pressure by moving across the river channel to islands or to nearby floodplain areas where hunting pressure was comparatively light or absent. Radio-collared females on the Elk Island and Seven Sisters areas either moved from or extensively within public hunting areas from the opening of pheasant season in mid-October through the end of the

deer season in late November or early December. One moved 16.1 km from her home range in the Elk Island area to an island near the mouth of Burns Creek but returned to her home range within 10 days. Marked females on the Intake unit commonly moved into cover along tributary streams during periods of harrassment. AARs for all females declined after November but remained higher during December-April than during May-August (Fig. 12). Michael (1965) observed little or no seasonal variation in movements of adult females in an unhunted population in Texas.

Yearling males were comparatively more mobile than other sex and age classes from June through November but less mobile than adult males from December through May. Mean monthly AARs were characterized by sharp peaks during June and November (Fig. 12). Breakup of family groups in June usually resulted in the male offspring leaving the ancestral home range. Such movement was observed among 4 of 5 radioed yearlings and included 3 dispersals and one temporary shift to adjacent uplands. The large AAR during November was probably influenced by small sample size (n = 4) and dispersal of one radio-collared individual.

Adult males were more mobile than adult females during all months except October and November (Fig. 12). However, like adult (3+) females but unlike both sexes of yearlings, monthly AARs of adult (2+) males were relatively stable throughout the year. Monthly means gradually increased from September to January, leveled off through April, and declined through August.

The greater mobility of males than females was consistent with findings of Carlsen and Farmes (1957), Thomas et al. (1964), and Michael (1965). Nelson and Mech (1984) also reported greater mobility of yearlings than adults in both sexes of deer.

Diel Patterns of Movement

The most distinct feature of movements throughout the diel period consisted of travel between wooded cover and agricultural fields. Deer used the same general areas of riparian habitat during diurnal periods and moved to the same fields during crepuscular and nocturnal periods (Herriges 1986). Those that shifted areas of diurnal use within seasons used the same fields as other deer in the new location.

During summer, diurnal movements of deer were minimal (Fig. 13), and crepuscular and nocturnal movements were typically to the nearest alfalfa field, usually within 0.5 km of riparian cover. Deer at Intake appeared to move to agricultural fields more consistently than deer in the Elk Island area. The proportion of nocturnal periods in which deer travelled to fields averaged 86% and 62% in the respective areas.

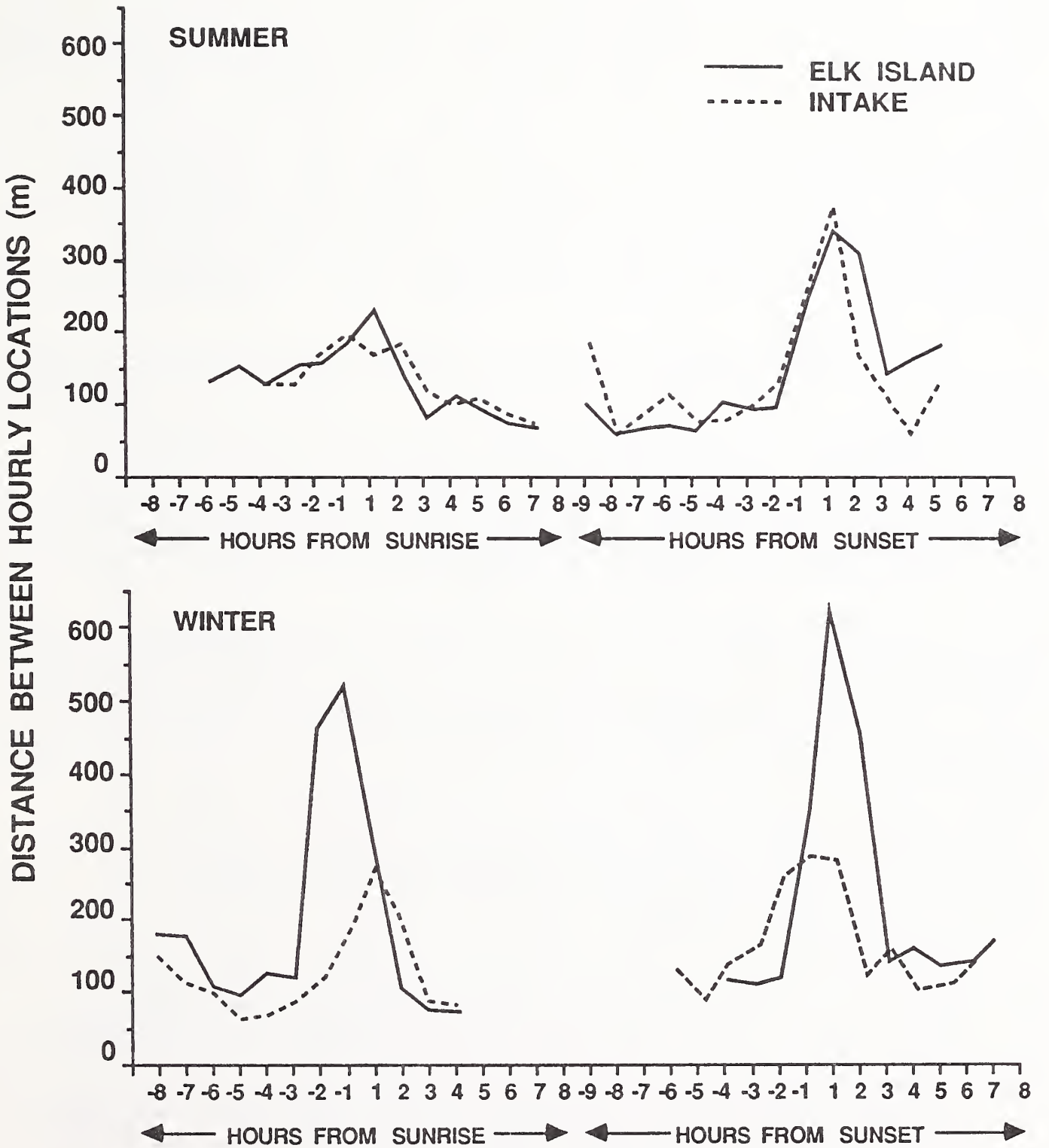


Figure 13. Mean distances moved between successive locations of deer during summer and winter on the Elk Island and Intake study units.

The proportion of deer moving to agricultural fields and the time spent in fields increased from early to late summer, especially for females with fawns. During mid-June, 7% of nighttime relocations of radio-collared adult females with fawns occurred in agricultural areas compared to 26% of those without fawns. These proportions increased to 22 and 44%, respectively, by early August. By early September, over half of all nighttime relocations of females were in agricultural fields. Fawns were first observed accompanying females to fields during late July-early August (Herriges 1986). Yearlings of both sexes and older nonproducing females visited fields more frequently and stayed longer per trip during early summer. Deer that spent diurnal periods in upland draws in the Intake area regularly traveled 2 km or more to the river bottom at dusk and returned before sunrise, whereas those that restricted their movements to the floodplain typically moved less than 0.5 km from bedding sites to fields.

The river appeared to impede movement of females with fawns until early August, and at least partially hindered movements of other deer. Minimal movement across the river channel during early summer may have been influenced by river flow which normally peaks in June and drops rapidly from July to August. Deer were often observed swimming across the river at dawn and dusk during late summer, although hourly radio-tracking indicated that individual deer did not make regular nocturnal movements across the main channel of the river.

A radioed adult female, that summered on a small area of Elk Island, did not move across the channel to agricultural fields when monitored over 24-hr periods during the summers of 1982 and 1983. Another, occupying an adjacent home range on the island and monitored only during 1982, also restricted her summer movements to the island. A third female, a 2-year-old with fawn, shifted her daytime activity off the island during late July 1983. During this same period an adult female on the main floodplain moved to and spent at least 1 hour in nearby fields during each nighttime tracking session in both summers. A radioed adult male remained on the island until 24 August and then moved to the mainland.

Hourly relocations at Intake during summer 1983 gave no evidence of deer crossing the river. However, relocations from periodic aerial flights indicated that 2 radioed adult females frequently crossed the river channel during summer and/or early fall. One, that did not successfully rear fawns during either 1984 or 1985, was located on either side of the river throughout the summer of both years. The other successfully reared fawns during the 3 summers, 1984-86, and did not cross the river until after mid August in any year.

During winter, movements of deer at Elk Island were generally more extensive than those of summer (Fig. 13) reflecting the greater average distance between diurnal bedding cover and fields at night. Deer at Intake did not exhibit the extensive movements during crepuscular periods during winter that were observed at Elk Island (Fig. 13). During winter as in summer, deer exhibited high fidelity to specific fields, the use of which appeared dependent on the location of diurnal bedding sites (Herriges 1986).

Radio-collared deer were located in agricultural fields during an average of 79% (40-100%) of all tracking sessions spanning 3 or more hours between 1800 and 0600 hrs. The time spent in fields ranged from less than 1 hour to an entire 12-hr period. Radioed deer commonly moved into fields at dusk and returned to riparian cover before daylight, consistent with large numbers of unmarked deer moving at those times. Deer using fields within 0.5 km of riparian cover were less likely to spend the entire night in fields than those travelling greater distances.

Daily movements at Intake during winter 1983-84 differed from those at Elk Island where all radioed deer spent the entire diel period on the river bottom. At Intake, 3 of 11 radio-collared deer spent the diurnal period on bottomlands and moved to fields on upland terraces in late afternoon; 3 others spent the diurnal period in upland draws and either traveled to the same fields or moved up the draws to feed in fields on the adjacent plateau; and the remaining 5 spent the entire diel period on the river bottom. Deer travelling to fields in uplands tended to move greater distances and remained in fields through most of the night, whereas those that remained on the river bottom usually traveled shorter distances and fed for shorter periods.

At Intake, deer moved from riparian cover to agricultural fields from mid afternoon through evening, while deer at Elk Island usually did not move from woody cover until dusk (Fig. 13). These differences may have been influenced by human disturbance. The Elk Island area had a higher density of farmsteads and other occupied dwellings than the Intake area, and also included an area open to public hunting. These factors, singly or in combination, may have modified daily movement/activity patterns of deer at Elk Island. Vogel (1983) reported a shift in activity patterns of deer from diurnal to nocturnal as a result of disturbance associated with homesite development. Although intensive farming and associated human activity did not preclude deer use of developed portions of the floodplain, it apparently influenced the time of day that nonforested areas were used.

Home Range Characteristics

Yearlong Home Ranges.-- Life home ranges, calculated from daytime relocations, for deer 2 years of age and older were 2.52 and 5.24 km^2 for females and males, respectively (AARs: 0.47, 0.91 km). There was no difference between the adult life AAR and the mean annual AAR for all years in which individuals were monitored ($P > 0.10$).

Mean annual home range size for deer with overlapping seasonal ranges was smallest for females 2 years and older and largest for yearling and older males (Table 24). Differences in home range by sex and age of deer were highly significant ($P < 0.01$): adult females < yearling females < all males (1+). Annual home ranges of yearling and adult males were not different ($P > 0.10$). Population size had no discernable affect on annual home range size for any sex and age class.

Nine radio-collared yearling and older females occupied discrete summer and winter home ranges; 6 were monitored for periods exceeding one year; 4 occupied the same discrete summer and winter ranges each year. One, that maintained the same winter home range during each of 3 years, summered in upland prairie as a 3-year-old before establishing a permanent summer home range on the river bottom. Another, that occupied the same summer range for 4 years, wintered in uplands as a yearling before establishing a permanent winter home range on the river bottom.

Among females, portions of annual home ranges occupied during autumn and spring were not used as consistently as areas occupied during summer and winter. Some adult females remained on summer/winter home ranges during those seasons, while others used areas common to neither seasonal home range. Hunting undoubtedly influenced portions of annual home ranges occupied during autumn. A radio-collared female, whose home range included a portion of the EIWMA, occasionally moved to the island in autumn during 1 of the 4 years she was monitored. Other marked deer exhibited similar variability in autumn movements. One female with discrete summer and winter home ranges made several exploratory movements to her summer home range during April-May in one year but remained on her winter home range through May of the next year.

Although some dichotomy in seasonal use of annual home ranges was apparent among adult (2+) males, most ranged widely and could be found in any portion of the annual range at any time of the year. The high mobility and variability in movements of yearling males from June-November indicated that most did not establish traditional summer home ranges immediately following breakup of family groups. By December, movments of yearlings were similar those of adult males (Fig. 12). Relocations from radio-collared yearling males in subsequent years indicated that most established permanent home ranges by their second winter.

Table 24. Characteristics of diurnal home ranges of white-tailed deer on the lower Yellowstone River bottom by sex and age from aerial surveys, 1980-85.

Season	Sex and Age	N[a]	AAR (km) $\bar{X}$	AAR (km) SE	Polygon (km^2) $\bar{X}$	Polygon (km^2) SE
Annual[b]						
	Females					
	Yrlgs.	12	0.72	0.16	4.81	2.20
	Ads.	43	0.47	0.03	1.14	0.11
	Males					
	Yrlgs.	2	1.04	0.09	--	--
	Ads.	5	0.91	0.11	5.24	1.48
Summer						
	Females					
	Yrlgs.	18	0.41	0.03	0.44	0.07
	Ad. (2+)	101	0.29	0.02	0.19	0.03
	Males					
	Yrlgs	6	1.18	0.29	1.11	0.57
	Ads.	27	0.56	0.05	0.79	0.12
Winter						
	Females					
	Yrlgs.	14	0.40	0.06	0.62	0.18
	Ads.	53	0.35	0.02	0.36	0.05
	Males					
	Yrlgs.	5	0.41	0.08	0.39	0.16
	Ads.	6	0.91	0.20	2.00	0.86

[a] N = number of animal seasons or animal years for each sex and age class (does not represent total number of animals involved).

[b] Annual diurnal home ranges includes only those individuals with overlapping summer and winter home ranges.

Annual diurnal home ranges of adult deer (Table 24), generally fell within the size range reported for nonmigratory white-tailed deer (Marchington and Hirth 1984). They closely approximated those reported by Gavin et al. (1984) for the lower Columbia River in southern Washington. Lower Yellowstone whitetails had much smaller annual and seasonal home ranges than reported for other eastern Montana areas including prairie (Wood

1987) and upland pine (Dusek 1987) habitats.

Seasonal Home Ranges.--Adult females consistently occupied summer home ranges from 1 June through 31 August and winter home ranges from 1 December through the end of February, though dates of movement between ranges varied between individuals and years.

Mean summer home ranges of yearling and older females were smaller than those of yearling and older males (Table 24). Adult males had smaller home ranges than yearlings. Differences between adult females and yearling females, yearling males, and adult males were highly significant ($P < 0.01$).

Summer home range size among females of age classes 1 through 3 may have been influenced by relative female density (Fig. 14), although differences within age groups were not significant ($P > 0.10$). Controlling for the effects of population size, there were differences ($P < 0.05$) in the AARs among ages, although age-specific responses to changes in female density varied and were not linear ($P > 0.10$, Fig. 14).

At low female density, AARs suggested decreasing home range size with increasing age, but the only difference ($P < 0.05$) was between yearling females and those 4 years and older. Home range size appeared to increase among all age groups from low to medium female density. At medium female density, home ranges of yearlings appeared larger than those of all older females, but differences were not significant. From medium to high density, home range size continued to increase among yearling and 2-3 year-old females, but a slight decrease was observed among mature and old females (Fig. 14). At high female density, differences among all age groups were significant ($P < 0.05$).

Winter home ranges were larger than summer home ranges for females and males 2 years and older, approximately the same size for yearling females, and smaller for yearling males (Table 24). Winter home ranges were larger ($P < 0.05$) than summer home ranges only for females 4 years of age and older.

As during summer, adult females had smaller diurnal home ranges than other deer during winter (Table 24). Differences between adult males and yearling and older females were highly significant ($P < 0.01$).

Diel Home Range.--Data from triangulation over 24-hr periods at Elk Island and Intake during 1982-84 indicated that nighttime movements substantially increased seasonal home range size. The mean diel polygon was twice as large as the diurnal polygon during summer and nearly 4 times larger during winter (Table 25). Despite this, the relationship between sex and age classes in diel home range size was similar to that of diurnal home ranges from both triangulation and aerial surveys (Tables 24 and 25): adult (2+) female home ranges were smaller ($P < 0.05$) than those of adult males, while ranges of yearling females appeared smaller than those of yearling males ($P = 0.07$). Among yearling and

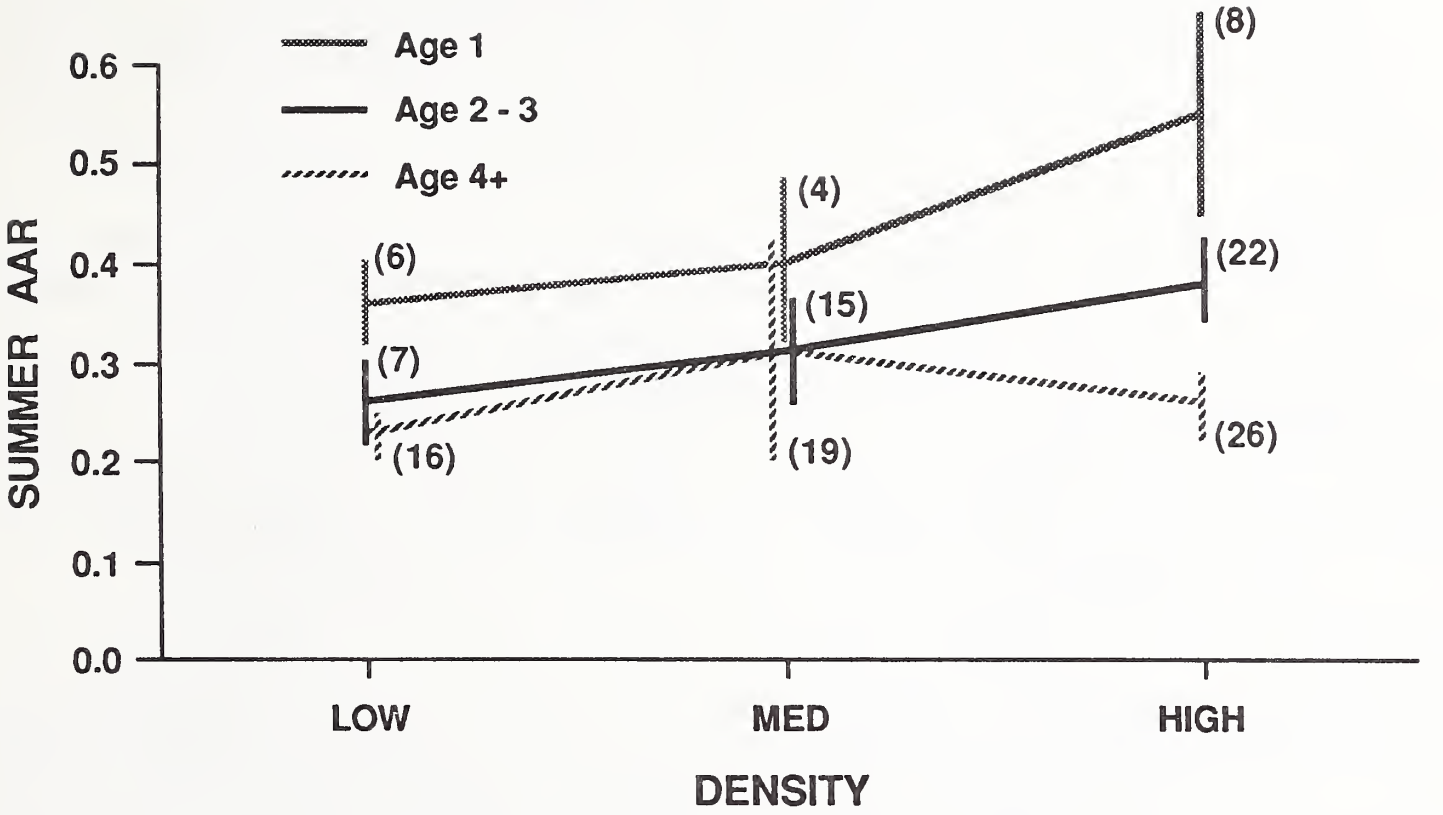


Figure 14. The relationship between summer home range (AAR) and density, and age of female white-tailed deer on the lower Yellowstone. Vertical lines represent ± SE of the mean.

older females, diel home ranges differed in size by season and age ($P < 0.001$).

Diel home ranges were markedly larger in winter than in summer among all sex/age groups (Table 25). Data from triangulation during summer, 1982 and 1983, suggested no apparent difference in diel home range size between 2-year-old and older females between the 2 years. However, population size also changed little between those years. Differences in diel home ranges of summer for females with and without fawns were not apparent.

Home Range Stability.--The straight-line distance (km) between consecutive GACs demonstrated the spatial relationship of, or fidelity to, seasonal home ranges for each of 35 females monitored for more than one year (Table 26). A distance ≤ seasonal age-specific AAR was interpreted to indicate little or no between-year change; 1-2 seasonal AARs represented a minor between-year shift; and, > 2 AARs reflected a major shift in seasonal home range or dispersal. Median distances for each age class illustrated trends during summer and winter (Table 26).

Table 25. Characteristics of diel and diurnal home ranges of white-tailed deer by season, sex, and age on the lower Yellowstone from hourly relcations by triangulation, 1982-84.

Season	Sex and Age	N	AAR (km) $\bar{X}$	AAR (km) SE	Polygon (km^2) $\bar{X}$	Polygon (km^2) SE
		Diel Home Ranges				
Summer						
	Females					
	Yrlgs.	4	0.55	0.03	1.74	0.22
	Ads.	27	0.31	0.02	0.87	0.08
	Males					
	Yrlgs.	1	0.87		3.28	
	Ads.	7	0.63	0.03	2.75	0.40
Winter						
	Females					
	Yrlgs.	7	0.69	0.11	2.76	0.79
	Ads.	11	0.62	0.08	1.82	0.26
	Males					
	Yrlgs.	2	0.97	0.14	6.72	1.49
	Ads.	3	1.18	0.40	6.22	2.45
		Diurnal Home Ranges				
Summer						
	Females					
	Yrlgs.	3	0.51	0.09	0.91	0.24
	Ads.	18	0.24	0.02	0.37	0.05
	Males					
	Yrlgs.	1	0.66		1.63	
	Ads.	3	0.65	0.06	0.86	0.18
Winter						
	Females					
	Yrlgs.	5	0.52	0.08	0.84	0.21
	Ads.	9	0.32	0.05	0.40	0.12
	Males					
	Yrlgs.	2	0.58	0.29	1.38	0.98
	Ads.	3	1.14	0.39	0.94	0.33

Table 26. Fidelity of yearling and older marked female white-tailed deer to summer and winter home ranges on the lower Yellowstone, 1980-85.

	Median Fidelity by Age Class							
	1 yr.		2 yrs.		3 yrs.		4+ yrs.	
Season	N	Median	N	Median	N	Median	N	Median
Summer	11	0.36(88)[a]	10	0.27(86)	11	0.22(79)	16	0.20(71)
Winter	8	0.73(182)	6	0.29(81)	8	0.47(134)	11	0.32(91)

[a] Median distance between successive GACs in km (fidelity index expressed as a percentage of the AAR for each age class).

Fidelity indexes (median distances expressed as percent of the age-specific AAR) suggested higher fidelity to summer than winter home ranges among females of all age classes (Table 26). This together with the relatively smaller home range size of summer (Table 24) indicated more intensive use of summer than winter home ranges. Similar findings were reported by Tierson et al. (1985).

Females in age classes 4 and older generally exhibited higher fidelity to seasonal home ranges than younger females (Table 26). This was particularly apparent in summer when home range fidelity stabilized as females approached 4 years of age. Interactions between age, distances between GACs, and season, however, were not significant (Chi-sq. = 8.75, 7 d.f., $P > 0.10$).

Dispersal

We considered dispersal to be individual movements beyond the limits of a home range that exhibited no predictable return (Bunnel and Harestad 1983). Our interpretation included establishment of a new home range discrete from the original, or ancestral, home range.

Movements were monitored at least through 18 months of age for 103 (63%) of 163 fawns captured and individually marked during 1980-84. Movements by 9 (17%) of 53 females and and 24 (46%) of 50 males suggested dispersal. The rate of dispersal was dependent upon sex (Chi-sq. = 10.12, 1 df, $P < 0.01$). Twenty-six deer were known to have dispersed as yearlings. Another 7 were not observed on their ancestral home ranges beyond autummn following their first birthday but presumably dispersed as yearlings.

Twenty-seven (82%) of 33 dispersers established new GACs on the river bottom, 6 moved into adjacent uplands. The tendency to remain on the river bottom did not vary between the 2 sexes of yearling deer (Chi-sq. = 0.42, 1 df, $P > 0.10$). The directions of movement by both dispersers and nondispersers from the GAC of ancestral home ranges were nonrandom (Chi-sq. = 26.96, 28.78, 11 d.f., $P < 0.01$). The resulting frequency distributions were bimodal on roughly a northeast-southwest axis which conformed to that of the river valley. Among yearlings which dispersed along the river valley, 13 moved upriver and 14 moved downriver.

Mean distances between ancestral and new GACs of dispersing yearlings were 19.5 km for females and 18.5 km for males; the difference was not significant (Chi-sq. = 2.77, 1 df, $P > 0.10$). Medians were 8.2 and 12.9 km, respectively. The longest yearling dispersal was 109.8 km by a female.

Yearling females appeared to disperse primarily during summer and males during late autumn. Among 14 yearlings for which month of dispersal was determined, 3 of 4 females dispersed during May-August, and 6 of 10 males dispersed during October-November. Of the other 19 yearling dispersals, 13 were taken by hunters outside ancestral home ranges. Some may have moved in response to hunting pressure, although the last observations of these deer on ancestral home ranges were made during May-September suggesting that some had dispersed prior to hunting seasons.

Dispersal of deer older than yearlings was uncommon. Two marked females were known to have dispersed as 2-year-olds. Both left the river bottom during May or June. A radio-collared female shifted her annual home range 3 km within the Elk Island unit when approximately 7 years-old.

The higher rate of dispersal among yearling males than females (46 vs. 17%) agreed with findings of Hawkins et al. (1971), Kammermeyer and Marchington (1976), Nelson and Mech (1984). Disproportionately high rates of dispersal among yearlings, particularly males, has also been documented for mule and black-tailed deer (Robinette 1966, Bunnell and Harestad 1983).

HABITAT SELECTION

Diurnal Habitat Selection

Deer selected ($P < 0.05$) riparian forest and shrub cover types and avoided ($P < 0.05$) agricultural and grassland types during daytime in all seasons (Figs. 15 and 16). Use of other types did not depart from availability ($P > 0.05$) or varied seasonally in analysis of use vs. availability (Fig. 15) and/or in the relative occurrence of types within 9-ha cells (Fig. 16).

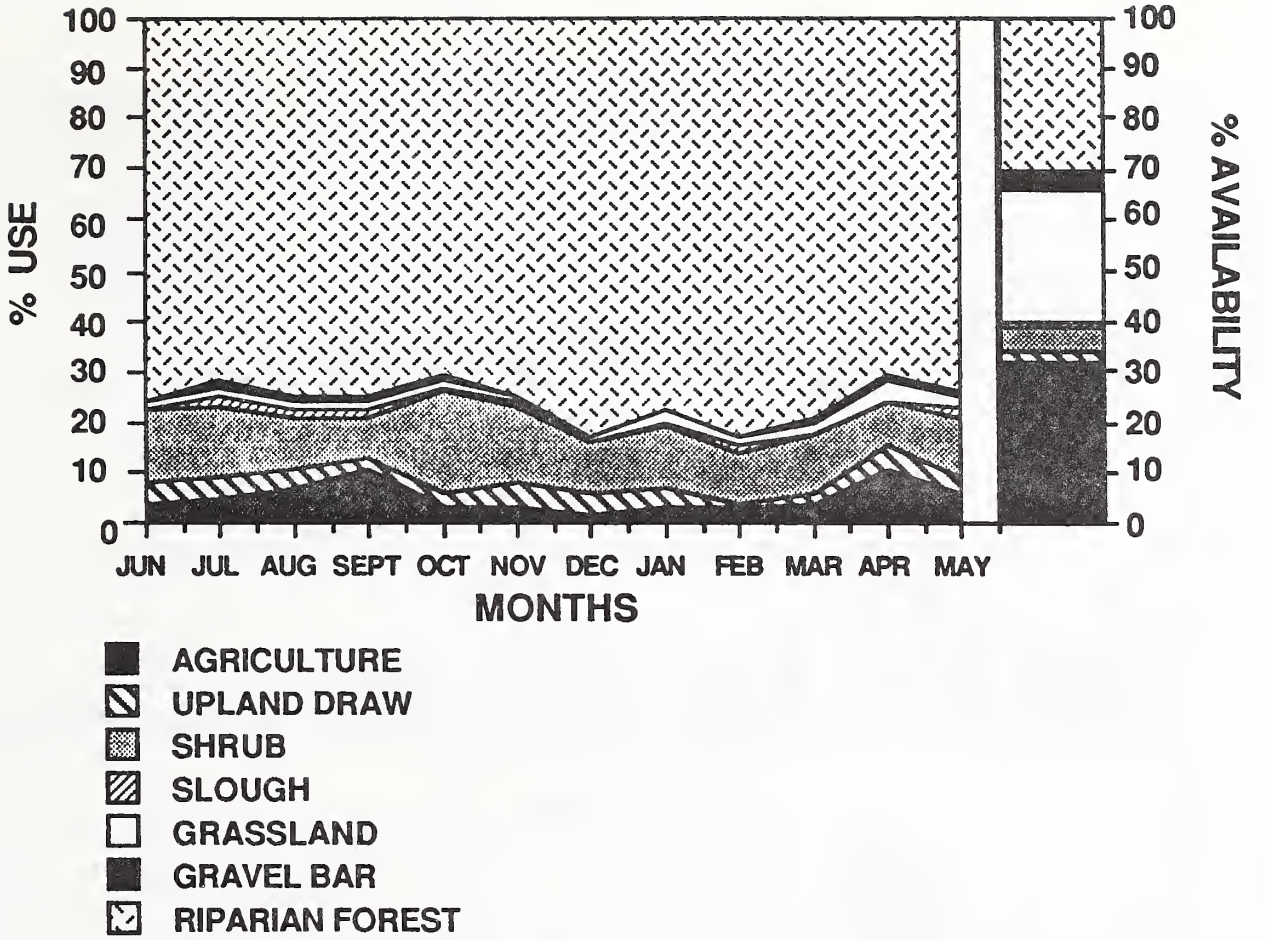


Figure 15. Use among cover types (%) relative to availability by radio-collared white-tailed deer from point locations from aerial surveys along the lower yellowstone River, 1980-86.

Seasonal variation in association of deer with riparian forest and agricultural types during daytime (Figs. 15 and 16) reflected the shift in distribution of deer from throughout the floodplain during summer to large patches of riparian forest near the river in winter. Riparian forest accounted for 75% of 1,394 relocations during summer and 80% of 887 relocations during winter. Agricultural fields accounted for 5% and 3% of all relocations during those seasons. All differences were highly significant ($P < 0.01$).

Habitat cells used by deer during summer contained less ($P < 0.05$) riparian forest (43%) than those used during winter (51%) and spring (47%). Also, cells occupied during summer, autumn and spring included more ($P < 0.05$) agriculture than those occupied during winter (20, 20, and 17% vs. 11%).

The summer-to-winter shift to riparian forest near the river was also reflected in the increased association of deer with streambed (water and sand/gravel bars) and with interspersed, successionally-related shrublands (Fig 16). Cells used by deer during winter and spring contained more ($P < 0.05$) shrubland than those used during summer; they also included more ($P < 0.05$) streambed than cells occupied during all other seasons.

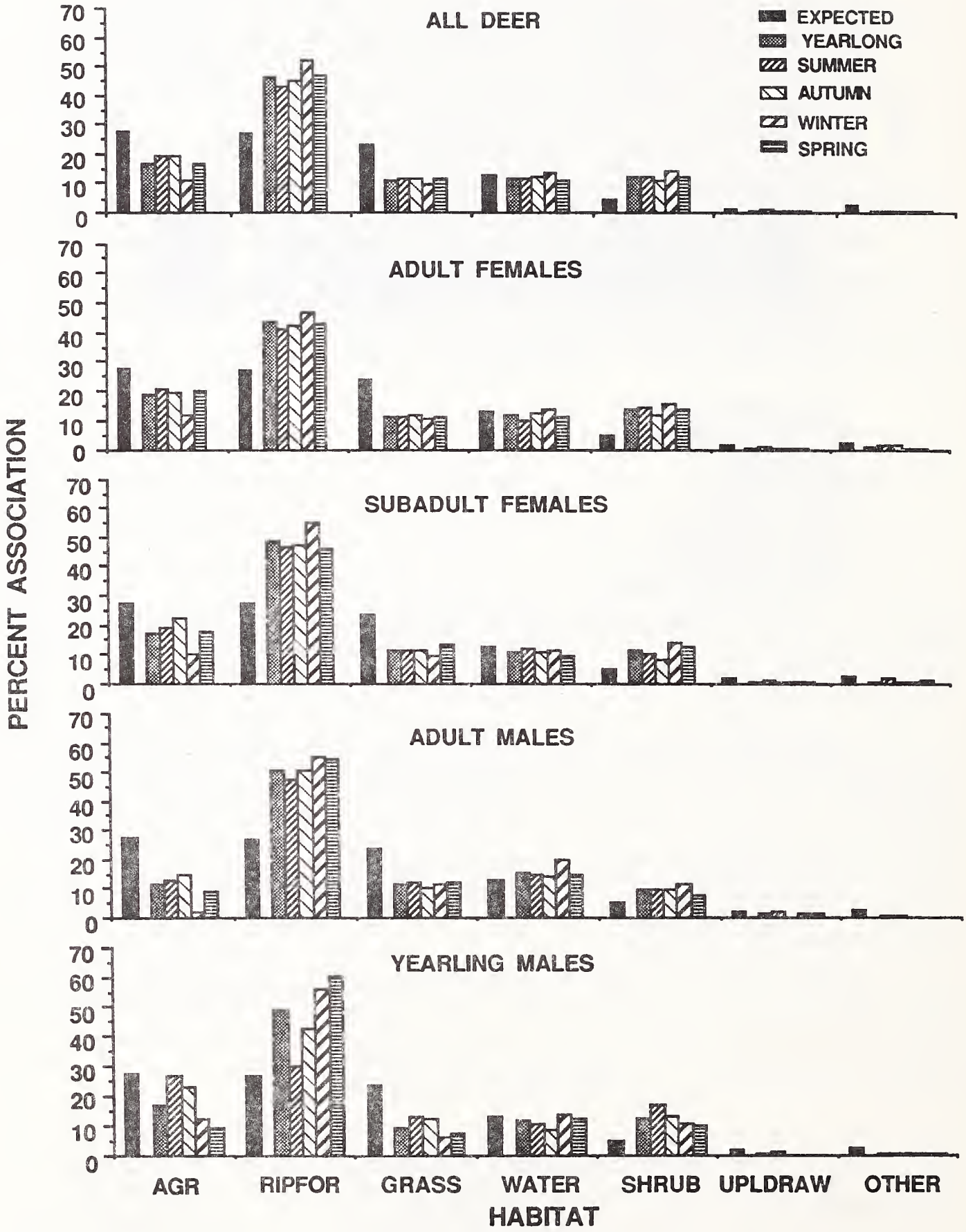


Figure 16. Relative abundance of cover types within 9-ha grid cells with which deer were associated compared to all cells. Data are partitioned by sex and age.

Of the 858 habitat cells on the 3 intensive study units, only 29% were occupied by individually marked deer in summer; while 27, 22, and 25% were occupied during autumn, winter, and spring, respectively. Unused cells contained more agricultural fields than those with documented use during all seasons (Table 27), but the only differences ($P < 0.05$) were in summer and autumn between cells with no documented use and those with 1-2 observations. Cells used intensively (5+ relocations) contained more ($P < 0.05$) riparian forest and shrublands than cells with little or no use during all seasons. They also contained less ($P < 0.05$) grassland than those with occasional or no use during all seasons but spring.

Although deer selected habitats with relatively large amounts of riparian cover, habitat diversity and interspersion of riparian with other cover types were important factors influencing habitat selection. The number of patches of cover and number of cover types were greater ($P < 0.05$) in cells occupied by deer than in unoccupied cells during all seasons (Table 27).

Spatial Relationships.--Although deer exhibited similar selection for riparian forest, shrubland, and agricultural types at Elk Island and Intake, diurnal relocations from triangulation indicated important differences in the use of specific communities (Table 28).

Among seral forest communities, deer preferred ($P < 0.01$) mature cottonwood at Elk Island during summer; use of younger forest communities either did not depart from availability or they were avoided. Use of mature willow and green ash did not depart ($P > 0.05$) from availability. Deer avoided all agricultural crop types during daytime.

At Intake, green ash was very highly selected ($P < 0.0001$) during summer. All other forest cover types were either used in proportion to availability or were avoided (Table 28). The absence of a well developed shrub understory in mature cottonwood stands may have discouraged use of that community. The apparent avoidance of mature willow was an artifact of the distribution of radioed deer away from the river where most willow occurred. During summer, deer at Intake also selected ($P < 0.05$) alfalfa fields during daylight periods, although most use of this type occurred shortly before sunset.

Analysis of grid cells indicated that deer at Intake were significantly ($P < 0.05$) associated with upland hardwood draws during summer. These draws occurred in close proximity to the river bottom and provided additional mesic sites that were attractive to deer and optimized spatial segregation of deer in summer, especially during years of high population density.

Table 27. Comparison of habitat characteristics among 858 9-ha blocks on the lower Yellowstone River that were unoccupied (0), used occasionally (1-2), or used intensively (5+) from relocations of individually marked deer, 1980-86.[a]

Habitat Characteristic	Summer			Autumn			Winter			Spring		
	0	1-2	5+	0	1-2	5+	0	1-2	5+	0	1-2	5+
% of Area in:												
Agriculture	31A	18B	23AB[b]	32A	19B	19AB	33A	16B	9B	32A	17B	20B
Grassland	27A	21A	11B	27A	22A	10B	27A	17A	8B	28A	18AB	9B
Riparian Forest	24A	33B	42C	23A	37B	47C	21A	43B	57C	22A	40B	47B
Shrublands	3A	9B	12B	3A	7B	13C	4A	8B	12B	3A	8B	13C
Upl. Draw	2A	2A	1B	2A	2A	0B	2A	2A	0B	2A	2A	0B
River Channel	13A	17A	10A	14A	13A	11A	13A	13A	14A	14A	15A	11A
$\bar{X}$ No. of:												
Habitat Patches	2.5A	2.9B	3.1B	2.3A	3.0B	3.0B	2.6A	3.0B	3.0B	2.6A	2.9B	3.0B
Cover Types	3.2A	3.8B	4.0B	3.2A	3.8B	3.9B	3.2A	3.9B	3.9B	3.2A	3.7B	$.0B
No. Blocks	609	141	108	626	143	89	668	117	73	640	131	87

[a] Numbers in parentheses represent numbers of data points in blocks or cells.

[b] Row values followed by different letters are significantly different ($P<0.05$) within seasons.

Table 28. Diurnal and nocturnal selection of bottomland cover types by white-tailed deer at Elk Island and Intake determined from relocating transmittered deer by triangulation.

	Elk Island						Intake					
	Summer			Winter			Summer			Winter		
Cover Type	A[a]	N	D	A	N	D	A	N	D	A	N	D
Seedling-Will./Cott.	0[b]	-	-	0	0	-	--	--	0	-	-	0
Y. Cottonwood	0	0	-	0	0	-	-	-	-	0	0	0
M. Cottonwood	++	++	++	++	+	+	0	-	0	0	0	+
M. Willow	+	0	0	+	+	0	-	-	-	-	-	0
Gr. Ash	0	0	0	0	0	+	++	++	++	++	++	+
Shrub	++	++	+	+	0	0	0	0	+	0	0	0
F. Pl. Grassl.	0	-	0	0	0	0	0	0	0	+	+	0
Cereal Grain	--	-	0	0	0		0	+	0	0	0	0
Sugar Beets	--	--		+	++	-						
Alfalfa	0	+	0	-	0	0	++	++	+	+	+	0

[a] A - diel period; N - nocturnal; and, D - diurnal.

[b] (0) indicates no selection ($P > 0.05$); - indicates avoidance ($P<0.05$); (+) indicates preference ($P<0.05$); and (--) or (++) indicates highly avoidance or preference ($P<0.01$).

During winter, deer at Elk Island selected ($P < 0.05$) mature cottonwood and shrublands (Table 28). The preference ($P < 0.05$) for green ash probably reflected increased use of the large island where the most extensive stands occurred. As during summer, deer avoided agricultural fields during daytime.

Deer also selected mature cottonwood and green ash communities at Intake during winter (Table 28). The occasional use of upland hardwood draws during daytime occurred while cattle were on bottomlands. Daytime use of agricultural fields occurred primarily in late afternoon on sites where cattle had recently been supplementally fed and in winter wheat fields on upland terraces adjacent to the bottomlands.

Sex and Age Relationships.--Selection for riparian forest, shrubland, agricultural, and streambed types differed ($P < 0.01$) with sex and age of the deer (Fig. 16). There also were sex-age related differences in deer use of various seral communities within the riparian forest ($P < 0.01$) (Table 29).

Table 29. Percent of seasonal relocations of transmitted deer by sex and age in individual cover types of riparian forest from aerial surveys, 1980-86.

Season, Sex and Age		Riparian Forest Cover Type				
		Willow/Cott. Thicket	Young Cott.	Mature Cott.	Mature Willow	Green Ash
Summer:						
Females:						
1-2 yrs.	(276)[a]	4	7	48	8	33
3+ yrs.	(527)	3	5	45	9	38
Males:						
1 Yr.	(38)	8	0	42	0	50
2+ yrs.	(180)	8	16	38	4	33
Autumn:						
Females:						
1-2 yrs.	(212)	7	9	41	9	34
3+ yrs.	(426)	9	8	44	8	31
Males:						
1 yr.	(35)	3	9	35	9	37
2+ yrs.	(132)	8	7	34	20	31
Winter:						
Females:						
1-2 yrs.	(239)	4	16	46	12	23
3+ yrs.	(348)	3	12	55	11	19
Males:						
1 yr.	(75)	5	33	36	9	16
2+ yrs.	(60)	5	28	47	7	13
Spring:						
Females:						
1-2 yrs.	(222)	2	17	40	11	30
3+ yrs.	(314)	4	7	50	9	30
Males:						
1 yr.	(89)	3	26	33	12	26
2+ yrs.	(54)	6	28	35	11	20

[a] Sample size for each sex and age by season.

Overall, habitats occupied by adult males during daytime contained more riparian forest and streambed than those occupied by other deer (Fig. 16). Within the riparian forest, adult males used the young cottonwood community to a greater extent than did females (Table 29). Cells occupied by mature females contained more riparian shrublands and agriculture than those occupied by other deer. Within the riparian forest, females were more associated with mid-to-late seral communities. Tests for sex-age differences in association with various habitat components indicated that mature females also used habitats with comparatively greater diversity and interspersion (more types and patches of each, $P < 0.05$) than those use by other deer.

Patterns of habitat selection among subadult females paralleled and were not different ($P > 0.05$) from those of mature females, overall or seasonally (Fig. 16). Those of yearling males paralleled females during summer and autumn, but more closely resembled adult males in winter and spring.

In summer, habitats occupied by yearling males contained more ($P < 0.05$) agricultural fields than those occupied by adult males, though differences in use of fields between yearling males, subadult females, and mature females were not significant ($P > 0.05$). The close association of these groups with agriculture was also apparent in their earlier appearance in fields; adult males rarely appeared in fields before dusk.

During summer, habitat cells occupied by yearling males included less ($P < 0.05$) riparian forest than cells occupied by all other deer. In winter, they contained more ($P < 0.05$) riparian forest and less shrublands than cells occupied by mature females. By spring, there were no differences ($P > 0.05$) in habitat use between yearling and adult males. During spring, cells occupied by yearling and older males contained less ($P < 0.05$) agriculture and shrubland types than those occupied by mature females.

Nocturnal Habitat Selection

Habitat use patterns and preferences after dark differed from those of daytime primarily in markedly greater use of agricultural fields and selection for specific crop and riparian forest cover types (Table 28). At Elk Island, where the most complete data were obtained, 27% of all nocturnal point locations from triangulation during summer and 64% of those in winter were in agricultural fields. Only 3 and 5% of all daytime relocations of radioed deer on the river bottom during 1980-85 occurred in fields in summer and winter, respectively.

Nocturnal patterns in selection for specific agricultural field or crop types differed seasonally and between the Elk Island and Intake areas (Table 28). During summer, deer selected alfalfa fields ($P < 0.05$) at both Elk Island and Intake. At Elk Island, 30% of all scanning circles around nocturnal point

locations contained alfalfa compared to 9% during diurnal periods. Spotlight surveys (Compton 1986a, Herriges 1986) indicated selection of alfalfa fields by deer among crop types.

At Elk Island, irrigated grain fields were avoided ($P < 0.05$) during summer. The preference for wheat fields at Intake (Table 28) appeared largely an artifact of selection by deer for alfalfa and riparian cover adjacent to wheat fields. The relative amount of edge per unit of wheat field area in scanning circles around deer locations was almost twice that of random scanning circles suggesting that most of these locations were not centered in the wheat fields. Spotlight surveys showed these wheat fields to be avoided by deer during summer (Herriges 1986).

During winter, alfalfa was selected at Intake (Table 28), while its use at Elk Island did not depart from availability ($P > 0.05$). At Elk Island, deer exhibited a preference ($P < 0.01$) for sugar beet fields. As in summer, the apparent selection for grain fields at Intake may have been an artifact of selection of nearby alfalfa fields as indicated by spotlight surveys (Herriges 1986).

Selection of fields during winter appeared to reflect availability of crop types and residues. At Elk Island, sugar beet fields were highly selected by deer at night even though fields used were often more than 1 km from riparian cover used during diurnal periods. Few alfalfa fields retained sufficient residual growth to attract deer following the harvest of 3 crops the previous growing season. Irrigated grain fields were plowed during autumn of most years also reducing availabilty of crop residues to deer.

Sugar beets were not grown at Intake, where available crop types were limited to alfalfa and grass hay and cereal grains. Use of grain fields, including stubble and seeded winter wheat fields on upland terraces, did not depart ($P > 0.05$) from availability. Selection of floodplain grassland at Intake (Table 28) was primarily attributable to deer using sites where cattle had been fed grain or alfalfa hay.

Deer continued to use riparian forest during nighttime at both study units, especially on bottomlands at Intake where fields were lacking or were heavily grazed by cattle (Table 28). At Elk Island, mature cottonwood and mature willow were selected, while use of other riparian communities did not depart from availability. Only green ash was selected during nighttime at Intake; use of other riparian communities did not exceed availability.

FOOD HABITS

Browse and agricultural crops dominated the yearlong diet of deer on the lower Yellowstone, accounting for 42% and 41% of the total volume of rumens, respectively. Browse received its highest use during January (69% by volume) and its lowest use during April (10%). Deer used agricultural crops heavily during August (41%), October (51%), November (52%), and April (75%) and minimally during May-June (8%). Forbs accounted for 7% of the yearlong diet; their relative volume in rumens increased dramatically from April (3%) to May (19%). Grasses, which accounted for 10% of the yearlong diet, were used in appreciable quantity only during March (19%).

Seasonal Trends

Leaves and the current year's stem growth of western snowberry, Woods rose, and willows accounted for nearly one-third of the summer diet (Table 30). Alfalfa was the most abundant single item contributing nearly one-third of the summer diet by volume and occurring in 12 of 15 rumens. No single naturally-occurring forb species was identified in more than 3 of the 15 summer samples, and aster (Aster spp.) was the only species contributing 1% or more of the seasonal diet.

Neither the average volume of browse nor individual species used changed appreciably from summer to autumn. Autumn use of western snowberry also included ripened fruit. The only major change in the diet from summer to autumn was decreased use of forbs with increased use of agricultural crops (Table 30). Alfalfa, which was heavily used during summer, was replaced by cereal grains and sugar beets during autumn. Yearlong use of beets was highest in October, coincidental to harvest, when they accounted for 30% of the aggregate average volume of 23 samples.

Browse dominated the winter diet and consisted of leaf detritus, buds, and woody stem tissue of plains cottonwood and western snowberry. Use of agricultural crops generally declined from autumn with sugar beets still predominating among crop residues. Alfalfa received its lowest seasonal use during winter and was present in only 16 of 45 rumens.

Browse received its lowest seasonal use during spring (Table 30). Species composition of browse changed from woody stem tissue and detritus from plains cottonwood during March to green leaves and succulent stem tissue of Woods rose and western snowberry during May. The average percent by volume of alfalfa increased from 3% in March to 44% in April.

Table 30. Annual and seasonal food habits of white-tailed deer on the lower Yellowstone River determined from rumen contents of 184 deer, 1980-86.

	Annual	Summer	Autumn	Winter	Spring
	(184)[b]	(15)	(76)	(45)	(48)
Taxa[a]	FR/VOL	FR/VOL	FR/VOL	FR/VOL	FR/VOL
BROWSE:					
Populus deltoides	68/17[c]	47/ 1	51/ 7	87/36	83/19
Prunus virginiana	12/ 1	40/ 2	13/ 1	7/tr[d]	6/tr
Rosa woodsii	52/ 4	100/ 8	50/ 4	64/ 4	27/ 2
Salix spp.	30/ 3	53/ 4	34/ 3	24/ 2	19/ 2
Symphoricarpos occidentalis	66/11	87/18	78/15	60/11	46/ 3
Unidentified Browse	51/ 5	60/ 3	49/ 5	49/ 5	52/ 5
Total Browse	99/42	100/40	100/38	98/60	96/33
FORBS:					
Unidentified Forbs	56/ 6	87/19	58/ 6	58/ 5	40/ 4
Total Forbs	67/ 7	93/22	72/ 7	62/ 6	52/ 5
GRASSES:					
Unidentified Grass	70/10	33/ 2	68/ 8	67/ 8	88/16
Total Grasses	71/10	33/ 2	68/ 8	67/ 8	88/16
AGRICULTURAL CROPS:					
Alfalfa	48/14	80/31	51/12	36/ 8	42/16
Cereal Grains	31/10	13/ 2	38/12	18/ 3	38/ 4
Sugar Beets	36/15	---	41/20	42/13	33/15
Total Agriculture	80/41	80/36	86/47	68/26	81/46

[a] Species comprising less than 3% volume or occurring in less than 25% of seasonal samples were omitted but used in calculating seasonal totals among forage classes.

[b] Seasonal sample sizes are in parentheses.

[c] % of seasonal samples that the item occurred in/ % of seasonal diet.

[d] tr = < 1%.

Spatial Relationships

Specific forage preferences and/or use reflected availability as influenced by local land use practices among 3 segments of river bottom within which rumens were collected: Glendive-Intake; Intake-Savage; and Savage-Sidney. Relative use among forage classes between the 3 segments during growing (spring, summer, and early autumn) and dormant (late autumn and winter) seasons suggested that agricultural crops replaced browse in the diet where crop residues were readily available (Table 31).

During the growing season, alfalfa was the major item used in all 3 segments of river bottom and occurred in at least two-thirds of the rumens from each segment (Table 31). Comparatively high use of agricultual crops and low use of browse occurred in the segment between Savage and Sidney. Five different crop types accounted for 4% or more of the diet from Savage to Sidney that compared to 2 crop types from Glendive to Intake and 1 from Intake to Savage.

Cereal grains accounted for an appreciably larger proportion of the diet during the dormant season in the segment of the study area between Glendive and Intake than elsewhere (Table 31). Stubble from dryland cereal crops, which occurred on the floodplain as well as adjacent upland terraces, was generally not plowed during autumn allowing deer access to waste grain. These, as well as hay lands, were also grazed by cattle throughout much of the period of vegetative dormancy.

The segment of river bottom between the diversion dam at Intake and Savage was characterized by a transition in land use; land use practices near Intake were devoted almost exclusively to livestock production, but intensive cropping of cash crops was progressively integrated into ranching operations downstream toward Savage. Many of the fields were occupied by cattle from late autumn through early spring. Although both sugar beets and alfalfa were grown, their combined use during the dormant season was approximately half that in the segment downstream from Savage (Table 31). A comparatively larger proportion of the diet consisted of browse compared to the intensively cultivated floodplain downstream from Savage (53 vs. 34%).

Agricultural crops dominated the diet of deer throughout the year in the segment of river bottom between Savage and Sidney which was characterized by intensive cultivation and minimal livestock use (Table 31). Sugar beets accounted for nearly one-third of the diet of deer during the dormant season and declined to half that amount during the growing season. The occurrence of cereal grains among rumens from portions of the study area flood irrigated from the Lower Yellowstone Project was minimal because autumn-plowing of stubble minimized the amount of crop residue available to deer. Pinto beans were grown only north of Savage and, thus, occurred only in rumens from that segment of river bottom.

Table 31. Food habits of white-tailed deer on the lower Yellowstone River by river segment during the dormant and growing seasons from rumen contents of 185 deer, 1980-86.

	Dormant Season		
	River Segment		
Taxa[c]	1[a] (45)[b] FR/VOL	2 (32) FR/VOL	3 (62) FR/VOL
BROWSE:			
Populus deltoides	73/25[d]	63/24	73/16
Rhus trilobata	11/ 1	22/ 1	16/tr[d]
Rosa woodsii	36/ 2	63/ 6	45/ 2
Salix spp.	31/ 4	25/ 1	27/ 2
Symphoricarpos occidentalis	56/ 9	63/14	69/ 7
Unidentified Browse	47/ 5	50/ 6	60/ 6
Total Browse	98/50	100/53	100/34
FORBS:			
Unidentified Forbs	24/ 2	63/ 7	61/ 4
Total Forbs	44/ 3	72/ 8	68/ 5
GRASSES:			
Unidentified Grass	73/ 9	75/14	66/10
Total Grasses	73/ 9	75/14	66/10
AGRICULTURAL CROPS:			
Alfalfa	22/ 9	34/ 5	53/10
Cereal Grains	60/27	22/ 1	29/ 5
Corn	4/tr	9/ 4	11/ 2
Pinto Beans	---	---	7/ 2
Sugar Beets	2/tr	38/15	77/31
Total Agriculture	71/36	66/25	92/49

Table 31 continued.

	Growing Season		
	River Segment		
	1 (23) FR/VOL	2 (3) FR/VOL	3 (20) FR/VOL
BROWSE:			
Populus deltoides	57/ 4	33/ 2	65/ 2
Prunus virginiana	30/ 2	---	20/ 1
Rosa woodsii	74/ 6	100/19	55/ 6
Salix spp.	35/ 3	---	35/ 5
Shepherdia argentea	9/ 1	67/ 5	10/ 1
Symphoricarpos occidentalis	83/21	100/18	55/ 8
Unidentified Browse	35/ 5	100/ 7	40/ 3
Total Browse	100/42	100/50	90/26
FORBS:			
Leguminosae	---	33/ 1	---
Melilotus officinalis	---	67/ 1	---
Unidentified Forbs	83/13	67/12	60/12
Total Forbs	83/15	100/13	75/12
GRASSES:			
Unidentified Grass	61/ 7	100/ 2	70/ 7
Total Grasses	61/ 7	100/ 2	70/ 7
AGRICULTURAL CROPS:			
Alfalfa	70/30	67/34	75/26
Cereal Grains	13/ 4	---	10/ 4
Corn	4/ 2	---	10/ 4
Pinto Beans	---	---	5/ 4
Sugar Beets	---	---	25/17
Total Agriculture	74/36	67/34	85/55

[a] River segments: 1). Glendive-Intake; 2). Intake-Savage; and 3). Savage-Sidney

[b] Sample sizes are in parentheses.

[c] Species comprising less than 3% by volume or occurring in less than 25% of samples were omitted but used in calculating totals amonng forage classes.

[d] % of samples that the item occurred in/ % of diet.

Sex and Age Relationships

Forage preference and/or use differed seasonally between adult males and females. Forage use by fawns of both sexes approximated that of adult females (Fig. 17); data were not available for fawns during the growing season. Agricultural crops, primarily alfalfa, dominated the diet of adult females during April-September, while adult males used more browse. Relative use of forbs and grasses did not differ between sexes. During October-March, males used more crop residues and less browse than females.

Factors Influencing Seasonal Food Habits

Yearlong food habits of white-tailed deer on the lower Yellowstone River apparently were influenced primarily by phenological changes in natural forage on the river bottom and relative abundance and variety of agricultural crops available to deer (Table 30). The relative amount of browse used during winter was comparatively less than that reported for bottomlands of the Missouri River (Allen 1968) or in mountain foothills (Martinka 1968) where alfalfa was the only major agricultural crop grown. Kamps (1969) also reported relatively low use of browse in mountain foothills where cereal grains were grown and utilized by deer.

Seasonal changes in crop types in rumens generally corresponded to shifts in relative use of fields (Compton 1986a). With the exception of alfalfa during the growing season, use of crops was largely of residues remaining after harvesting. Agricultural crops primarily replaced browse in the diet and were used most heavily where agricultural lands were flood irrigated and where livestock use of fields and natural floodplain areas was minimal or absent (Table 31). Compton (1986a) reported that regular use of individual fields during winter was contingent upon availability of crop residues and absence of livestock grazing following harvesting of crops.

Summer food habits of white-tailed deer on the lower Yellowstone were similar to those reported by Allen (1968) for Missouri River bottomlands in central Montana. Use of natural occurring forbs in both riverine environments was similar to that in ponderosa pine uplands of southeastern Montana (Dusek 1987) but considerably less than in mountain foothills of central Montana (Martinka 1968, Kamps 1969). The comparatively low use of natural herbaceous material in riverine and pine habitats in eastern Montana during summer, along with correspondingly high use of succulent browse, may not only reflect influence of abnormally dry years during this study but also differences in longterm precipitation patterns between mountain foothills and other habitats in eastern Montana. Use of alfalfa was high in all habitats where it was readily available regardless of the relative use of forbs.

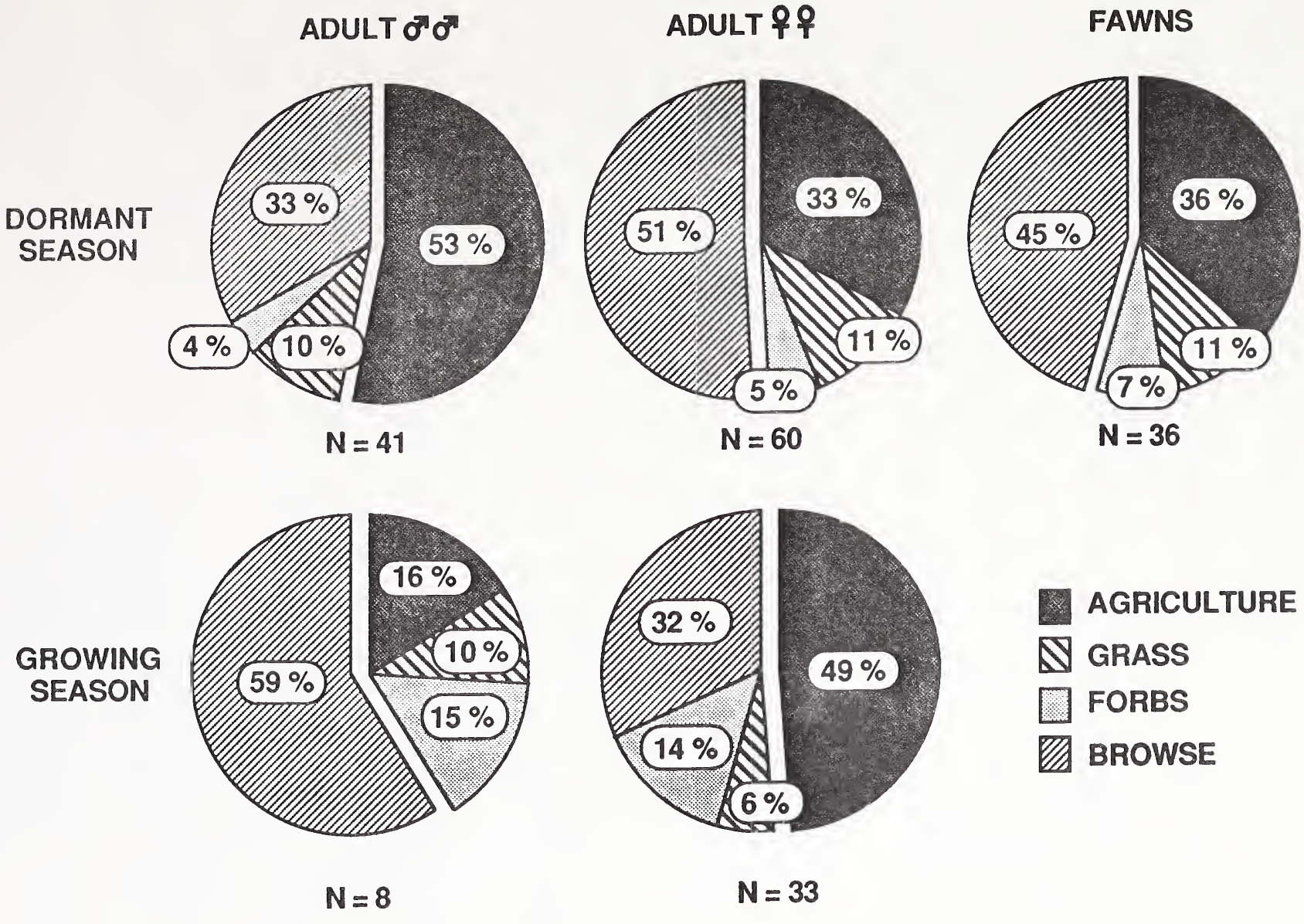


Figure 17. Use of forage classes by fawn, adult male, and adult female white-tailed deer on the lower Yellowstone during periods of vegetative growth and dormancy, 1980-86.

Woody stem tissue and leaf detritus have comparatively lower digestibility than green or succulent forage with greater proportions of readily digestible carbohydrates (Segelquist et al. 1972, Harlow et al. 1975). Coblentz (1970) and Suring and Vohs (1979) suggested a preference for green herbaceous forage by deer during winter and that heavy use of browse may occur only in the absence of green herbaceous forage.

The observed pattern in forage use between sexes of adults may have reflected energetic costs during late gestation and lactation among females and the period following breeding among males. Because fawns accompanied adult females through the period of vegetative dormancy, their foraging habits would be expected to be similar.

DEER-HABITAT RELATIONSHIPS AND POPULATION REGULATION

White-tailed deer-habitat interactions and relationships along the lower Yellowstone River can be examined from two broadly different perspectives: 1) their role in determining general patterns of distribution and abundance, and 2) their influence on deer population dynamics. The former addresses how populations have come to be what they are and their general status today; the latter how they operate.

Habitat Influences on Distribution and Abundance

The current widespread distribution and abundance of white-tailed deer on the lower Yellowstone and other riverine habitats of the northern Great Plains apparently reflect significant changes in the characteristics of these habitats. Historical records suggested that whitetails occurred only sporadically in low numbers within a habitat-environmental complex that was very different from today.

Mid-to-late 19th century descriptions and photographs (e.g., Brown and Felton 1955) indicate a sparsely wooded floodplain with little or no shrub understory similar to that described by Crouch (1979) for the South Platte River. Such conditions apparently resulted from heavy use by large numbers of bison and other native ungulates, highly variable subsurface water flow, frequent fires, and natural succession toward climax grasslands. Intensive grazing of riparian bottomlands has been shown to alter stream morphology (Platts 1979) and drastically reduce or eliminate understory cover (Severson and Boldt 1978, Crouch 1982, Smith and Flake 1983). Severson and Boldt (1978) also indicate that growth of woody vegetation on tree-dominated floodplains "was almost certainly limited to some extent by fire."

Within that vegetation complex, the riparian forest and shrub habitats favored by whitetails were likely very limited. Without irrigation in a region characterized by variation in climatic and other environmental conditions, resource outputs and availability would have varied extremely. In addition, the presence of large numbers of bison, elk, and other wild ungulates probably imposed competitive resource partitioning among species and further limitation on resource availability and use by whitetails. Similarly, the presence of predators, including wolves, could have excluded deer from areas lacking suitable cover. Under such conditions white-tailed deer could have been relegated to a relatively narrow niche with wide spatial and temporal fluctuations in distribution and abundance.

Elimination of bison and extirpation or reduction in the numbers of other wild ungulates in the region, settlement and development of agriculture along rivers, and construction of irrigation systems apparently all contributed to development of more extensive, diverse habitat along the floodplain. Crouch (1979) attributed development of a 1-km-wide belt of riparian

forest with a dense shrub/herb understory on the South Platte by the mid 20th century to similar physical and biological factors associated with settlement and subsequent trends in land use. Water management that provided yearlong surface and shallow subsurface water flow was especially important. The construction of large-scale irrigation systems along the lower Yellowstone may have resulted in shallower and more stable subsurface water flows that enhanced cottonwood survival and shrub/herb growth on bottomlands. However, agricultural practices that precluded or limited livestock grazing primarily to autumn and winter also abetted development of the cottonwood sere.

These changes provided more extensive habitat and a broader ecological niche for whitetails. Together with predator control and restricted hunting, they set the stage for rapid expansion of populations by the 1940s and 1950s. Today, deer occur more or less continuously throughout the length of the Yellowstone and other major rivers and tributaries in eastern Montana. Although populations vary spatially and fluctuate somewhat over time, densities are generally high.

Mackie (1983) related high density and stablity in mule deer populations in the northern Rocky Mountains and Great Plains to complex, diverse habitats with stable resource outputs; progressively lower densities and greater variability were associated with progressively simpler and more variable environments. These relationships may also apply to white-tailed deer in the northern plains and explain temporal and spatial variation in population densities along the lower Yellowstone.

Riverine environments in the northern plains today represent microcosms of relatively high complexity, diversity, and stability within a region characterized by relative simplicity and high variability in environmental conditions. High complexity and diversity are provided by interspersion of relatively small units of many different vegetation types or communities, land uses, and agricultural practices. Stability is inherent in the sense that, on the average, resource availablity and outputs remain high and predictable over time within small, local areas. Gavin et al. (1984) imply similar interpretation in referring to stability or constancy of deer habitats along the lower Columbia River.

White-tailed deer densities on our study area, that ranged from 14 to 26/km^2 in autumn, were substantially higher than estimates for nearby upland habitats during 1980-86. Autumn densities for a population resident to a prairie habitat never exceeded 1/km^2 (Wood 1987). Density of another population on prairie-agricultural habitat was estimated as 5/km^2 during spring 1983, when whitetails were generally reaching a recent, if not an all-time peak in numbers throughout eastern Montana (Dusek et al., unpubl.). Deer densities also varied spatially within our study area -- from less than 15 to approximately 50 deer/km^2 among segments of river bottom during 1985 (Compton et al. 1988). Differences in the relative abundance of deer along the river

bottom were directly related to the abundance of riparian forest and shrub habitat. The relative abundance of riparian cover may also have been an important factor influencing differences in deer densities between the river bottom and prairie/prairie-agricultural habitats. Riparian draws comprised only 3% of the prairie habitat (Wood 1987) and 7% of the prairie- agricultural area (Dusek et al., unpubl.), while riparian communities covered 24-40% of our 5 intensive study units (Table 3). However, these relationships between amount of riparian cover and deer density may be somewhat misleading. They could also be indicative of broader habitat/environmental differences that collectively influenced the occurrence and abundance of deer within and between the river bottom and uplands.

Development of riparian vegetation along the river followed the cottonwood, willow, and green ash seres that originated on small sand-gravel bars. As the amount of riparian cover increased, complexity and diversity also increased as a result of increased numbers and interspersion of small stands of all seral stages. Bottomlands characterized by extensive riparian forest and shrublands were typically interspersed by irrigated agricultural fields varying in size, crop type, and cropping practice. Riparian cover in the uplands consisted largely of the green ash type (Nelson 1961) in narrow stands along draws and ephemeral stream courses. These stands were only broadly interspersed by adjacent mixed- or bunchgrass-prairie, dryland grain, or, occasionally, dryland or streambottom alfalfa fields. Increased amounts of riparian cover between areas or habitats largely reflected increased topographic/physiographic diversity.

The importance of diversity and stablility in the occurrence and abundance of whitetails along the lower Yellowstone was also attested by high fidelity to bottomlands as compared with only sporadic, seasonal use of more monotypic uplands and ephemeral tributary drainages. It was also evident in limited daily and seasonal movements and relatively small home ranges on the river bottom. Uplands and drainages on our study area apparently did not fully meet diel or yearlong habitat needs. Their greatest and most consistent use occurred on the Intake area, where wooded draws and croplands were interspersed on benchland or terraces immediately adjacent to patches of riparian forest on the river bottom. Here, some deer bedded in draws during daytime and moved short distances to feed on bottomlands at night; during winter, others moved from bottomland riparian cover onto terraces to feed in grain fields.

Gavin et al. (1984) suggested that the sedentary nature and small home ranges of adult females were tactics reflecting adaptation to a stable habitat-environmental regime under which the most efficient behavior would be to remain on a familiar piece of range large enough to provide adequate food and cover.

Our findings generally agreed with that interpretation -- high fidelity of adult females to small home ranges on bottomlands was clearly related to diversity and interspersion of riparian and

agricultural communities providing high quality forage and cover on small areas. Habitats with high plant species diversity, including dicotyledonous forbs and shrubs, provides the greatest option for selective feeding by largely concentrate selectors such as the whitetail (Klein 1985). A pattern of habitat usage that included relatively dispersed distribution and limited movement within high quality forage-cover complexes during late spring and summer could optimize opportunity to sustain high female densities and successfully rear fawns. As with roe deer (Capreolus capreolus) (Klein and Strandgard 1972), the quality of local food-cover complexes available determines the minimum size of home range needed by white-tailed deer; the amount and quality of habitat overall determines how many home ranges an area may support.

Behavioral spacing of females in a complex and diverse environment during a period of optimal resource availability and output may allow white-tailed deer to attain comparatively high population density as postulated for waterfowl (Patterson 1976). Agonistic interaction among adult females prior to and during fawning may serve as a spacing mechanism (Gavin et al. 1984) and lead to dispersed distribution of females throughout available habitats. Interaction between mature females and other deer may also facilitate habitat or resource partitioning resulting in occupancy of the choicest, most productive habitat by mature females.

The relatively dispersed distribution of deer on our study area during summer reflected a dichotomy in habitat selection, and perhaps different habitat requirments between adult females and males. Differences in food habits probably reflected different physiological cycles between male and female deer (Fig. 17) as reported for other cervids (Watson and Staines 1978). Dense overhead cover was selected yearlong by all deer, but comparatively greater use of mature cottonwood stands by females and younger seral communities by males suggested that a dense understory was less important to males. The ecosystem nutrient content increased through succession, peaked in the mature cottonwood sere, and declined with the senescence and disappearence of the cottonwoods (Boggs 1984). Females were more closely associated with agriculture as indicated by habitat selection and food habits during the growing season. The vegetative and structural diversity, that characterized habitats selected by adult females, emphasized the importance of edge. Williamson and Hirth (1985) correlated edge with an optimal foraging strategy that was consistent with relatively limited movements and use of small seasonal home ranges by adult females on the lower Yellowstone.

Relatively lower fidelity to home ranges (Table 26) and greater mobility of subadult than mature females suggested the former may have been excluded from optimal habitat complexes. Yearling males may also have occupied suboptimal habitats during early summer, as suggested by patterns of habitat use, high and variable movement indexes, and variability in body and antler

growth. While summer movements of yearling males were generally greater than those of subadult females, habitat preferences were more similar to young females than to adult males. Forage-cover complexes undoubtedly varied in quality both spatially and temporally as influenced by environmental variability and/ or use by livestock. Compton (1986b) indicated that heavy grazing reduced shrub cover, primarily that of snowberry and rose, regardless of season, though summer grazing apparently reduced shrub cover to a greater extent than winter grazing.

Assuming that longterm seasonal use of pastures by livestock physically and biologically altered habitats preferred by deer (Severson and Boldt 1978, Smith and Flake 1983), nongrazed areas may have favored establishment of home ranges that socially dominant females could successfully occupy with predictability over time. In segments of river bottom receiving extensive autumn-winter livestock use, adult females attempted to compensate for physical alteration of mid-seral riparian communities by using sites near agricultural fields during summer that structurally met requirements for successful fawn rearing. Huegel et al. (1986) characterized fawn bedsites in the Midwest to include a tall, dense herb/shrub understory and dense tree overstory, irrespective of species composition, that provides visual isolation and comparatively cool microenvironments. The greater mobility of adult males than females and a more general pattern of habitat selection perhaps rendered them less sensitive to the effects of livestock.

The relationship between deer and agriculture, that included temporal and spatial variation in seasonal use of crops and movement between cover and fields, reflected relative availability of forage crops as influenced by cropping practices as well as seasonal changes in the behavior of deer. Alfalfa, the principal crop type used in summer, occurred throughout the river bottom often in the same fields for several years in succession. Because of this, and the dispersed distribution of deer during summer, alfalfa fields tended to be used more or less "traditionally" as an integral part of the summer home ranges of deer associated with adjoining riparian cover. Food habits of deer during the growing season (Table 31) indicated that alfalfa comprised approximately one-third of the summer diet throughout the river bottom study area. Diel movement patterns at Elk Island and Intake were most similar during summer (Fig. 13); both suggested minimal spatial variation in the relationship between deer and agriculture during that season. Intensities of use of individual fields varied with the amount and location of adjacent riparian cover. Generally, the relatively dispersed and stable use of alfalfa fields by individual and small family groups of deer associated with adjacent cover minimized opportunity for intensive use of individual fields except where isolated fields occurred in proximity to high quality riparian cover in which deer densities were locally high.

The relationship between deer and agriculture changed greatly from summer to winter when deer were distributed primarily in large stands of riparian forest near the river. Harvest and post-harvest treatment (plowing, grazing, etc.) of fields greatly affected the kinds, amounts, and distribution of crop residues available to deer through the winter as also reported for agricultural habitats in the Midwest (Murphy et al. 1965). Distribution of crop types used by deer during winter, that included sugar beets, small grains, and corn, varied spatially along the river bottom and was reflected in seasonal food habits (Table 31). Because of this, and the fact that these crop types were rotated among fields between years, winter use of fields tended to be more opportunitistic, intensive, and variable than summer use.

Habitat Influences on Population Dynamics

During winter, diel movements, habitat use, and food habits suggested a strategy of survival involving high energy input through selective foraging. Morphological attributes of deer allow them to increase selectivity as long as benefits outweigh energetic costs (Hanley 1982). Thus, such a strategy implied abundant and/or diverse forage resources (Klein 1985) and may be typical where deer have access to agricultural crop residues during winter.

Seasonal trends in condition, mortality, and reproduction indicated that white-tailed deer on the lower Yellowstone generally existed on a high nutritional plane, especially during winter. Measurements of diastemal and antler growth suggested that yearling males from the Yellowstone Basin existed on a higher nutritional plane than those in pine habitat in southeastern Montana (Swenson and Stewart 1982).

Females and fawns on the lower Yellowstone River maintained their respective body weights of late autumn through mid-to-late winter, while yearling and older males experienced weight loses corresponding with fasting during the rut. These trends were similar to those reported for supplementally fed deer (Ozoga and Verme 1982). Nutritionally stressed fawns experience substantial overwinter weight loss (Severinghaus 1981). The seasonal pattern of accumulation and mobilization of body fat, as expressed by the KFI (Table 8), closely paralleled that of whole weights (Table 7). The generally low rates of mortality among all sex and age classes during winter-spring (Table 16), and the lack of a direct correlation between winter severity and mortality, also indicated that deer wintered on a relatively high nutritional plane.

Strong fidelity to summer home ranges and resource partitioning that provided stable and diverse cover/forage complexes was probably important in minimizing variation in reproductive performance among adult females. During late spring-early summer, when social interaction among females was most intense, availability and use of naturally occurring

herbaceous forage was at a yearlong high. The availability of irrigated alfalfa on the river bottom may buffer shortages of natural forage during dry years on reproduction that may contribute to higher reproductive output on the river bottom than observed on prairie rangeland by Wood (1987). The comparatively close association of females with agriculture during summer optimized opportunity for selective foraging when the physiological demand on lacating females was highest (Short et al. 1969).

Socially influenced resource partitioning may allow dominant females use of habitats during spring-summer that assure optimal reproductive output often at the expense of younger females being forced into habitats with marginal forage/cover quality. The high association of yearling males and subadult females with agriculture during early summer may reflect interacting influences of resource partitioning, yearly variation of forage quality/abundance, and adult female density. Although all females were closely associated with agriculture during summer, a stategy favoring exclusive use of the choicest forage/cover complexes by socially dominant females, when physiological demands were highest, was consistent with high reproductive performance among mature females (3 through 7 yrs.), particularly age classes 6 and 7 (Table 14).

The comparatively high ovulation and fetal rates of adult (2+) females from the lower Yellowstone overall (Tables 11 and 12) compared favorably with those of supplementally fed females that were on a high nutritional plane (Verme 1969, Ozoga and Verme 1982). The high ova loss among females of 4 years and older was consistent with the "flushing" phenomenon (Ransom 1967, Roseberry and Klimstra 1970, Mansell 1974), suggesting that nutritional quality prior to breeding was sufficient to insure optimal reproductive potential among mature females.

Increasing social competition among females with density may explain yearly variation in recruitment and the greater sensitivity to variation in female density among ages classes 2 and 3 with respect to their reproductive performance. The interacting influence of density and environmental variability may also explain the more variable pregnancy rates among yearling females. Despite comparatively low reproductive potential among young adult females, about two-thirds of the 2 year-old females successfully reared fawns. Winter forage resources were obviously adequate to allow young females to successfully rear fawns, often at the expense of immediate body growth (Dusek et al. 1987).

Differences between pregnancy rates of yearling and older females were probably nutritionally influenced. More variable pregnancy rates among yearling than older females (Table 10) may have reflected yearly variation in availability of native herbaceous forage during summer. Years of relatively low pregnancy rates among yearling females generally followed years with abnormally dry growing seasons (Fig. 2). Lower pregnancy,

ovulation, and fetal rates suggested nutritional stress prior to breeding following growing seasons characterized by markedly below normal precipitation. Such pronounced effects of reduced nutritional plane have been documented for both free-ranging and confined populations of white-tailed deer (Morton and Cheatum 1946, McGinnes and Downing 1977, Kie et al. 1980). A greater sensitivity of the youngest breeding age class of females to influences of nutrition on reproduction was reported for deer (Julander 1961, Ransom 1967, Verme 1969) and other ungulates (Bergerud 1971, Skogland 1985).

The slight decline in pregnancy rates among subadult females from 1983 to 1984 (Table 10) coincided with a decline in body size among yearling males as expressed by diastemal length (Table 9). Body growth among yearling males appeared influenced by interaction of adult female density with environmental factors influencing forage production. If growth among yearling females was similarly affected, such interaction may also explain lower and more variable pregnancy rates among this age class. Nutritional stress may have inhibited physiological development among some females whereby they failed to conceive during the following autumn breeding season. A relationship between body weight and fertility was reported for young red deer (C. elaphus) hinds reflecting increased forage competition at high densities (Albon et al. 1983).

Lower longterm rates of recruitment at Intake than at Elk Island may have been influenced by habitat conditions related to grazing by livestock, diversity and availability of agricultural crops, and female density. Reproductive performance at Intake was characterized by lower fetal rates and a larger proportion of summer fawn mortality than at Elk Island (Table 15). There may have been fewer sites favoring successful recruitment of fawns to autumn at Intake, a situation severely aggravated at high female density. Deer density was higher at Intake than at Elk island from 1981 to 1984 despite the more widespread presence of cattle and lower consumption of agricultural crops by deer at Intake. However, when female density was markedly reduced in both areas in 1984 and 1985, recruitment rates at Intake did not increase to the extent of those at Elk Island.

The mechanics of density dependence on reproductive output apparently differed between the respective subpopulations. Comparatively high ovulation and fetal rates for both yearling and older females at Elk Island (Tables 12 and 15) suggested minimal nutritional deficiencies with little influence on potential productivity. Thus, net productivity was almost entirely influenced by adult female density as it influenced survival of fawns to 4 months of age.

Conversely, the lower pregnancy rates (Table 4), as well as lower fertility and fecundity (Table 12), at Intake were probably nutritionally influenced as a result of interaction between total numbers of adult females and environmental variables influencing quantity and quality of forage resources. Markedly lower rates

of recruitment among all age classes of producing females during all years combined may have reflected higher female density at Intake. Demographic differences in reproductive potential or recruitment of fawns to autumn between subgroups of a population may reflect environmental variation or differences in density, neither of which is mutually exclusive (Dapson et al. 1979).

Population Regulation

Traditional theory concerning deer-habitat relationships and population regulation has centered on the concept of a more or less determinate carrying capacity (K) linked to the standing crop of forage through density-dependent interaction (Caughley 1976, McCullough 1979). A general interpretation related deer numbers and dynamics to supply and optimum utilization of winter forage in northern environments (Dasmann 1971, Severinghaus 1979), although summer forage quality may similarly affect numbers and dynamics in hot, dry environments (Anthony 1976, Kie et al. 1980). McCullough's (1984) "black box" (stock recruitment) models for white-tailed deer prescribe a direct density-recruitment feedback relationship through resource availability influenced by deer use. Implicit in this relationship are decreasing animal size and condition and increasing mortality with increasing population size. Our findings provide basis for evaluating the application of these concepts to habitat relationships and regulation in white-tailed deer populations along the lower Yellowstone River and in other riverine environments in the northern Great Plains.

The general applicability of traditional theories has been questioned with regard to the role of predation (Peek 1980, Gasaway et al. 1983) and environmental variation (Wehausen et al. 1987, Wood 1987). Several alternative hypotheses integrate population regulation with social behavior. A "social fence" hypothesis (Hestbeck 1982) involves regulation through emigration at low densities and forage exhaustion at high densities. Gavin et al. (1984) implicated availability of suitable home ranges as a limiting factor, but once filled, females would be subject to the effects of habitat deterioration. Christian and Davis (1964) documented substantial mortality of Sitka deer (C. nippon) indirectly resulting from an endocrine response to density-related social stress, a phenomenon that has not been documented for indigenous North American cervids.

Our findings were not consistent with a hypothesis of regulation through winter forage carrying capacity. Strategies of habitat use, biological parameters, and population characteristics and dynamics all indicated that neither quality nor quantity of winter habitat limited population size. A strategy of selective foraging during winter, attended by extensive daily movements from riparian cover to agricultural fields and negligible overwinter mortality indicated that the population wintered on a high nutritional plane. Availability and use of agricultural crops by deer during autumn-winter did

not support the traditional concept of "limitation" through winter forage resources. Browse species used by deer during winter, primarily cottonwood and snowberry, were not limited in distribution and/or abundance. Deer appeared to be relative specialists in their use of browse species and agricultural crops during winter. This was a departure from the traditonal "forage generalist" strategy of deer in northern climates during winter (Nudds 1980).

Influence of Density.--Density dependence on the lower Yellowstone appeared to manifest itself primarily in the rate of recruitment of fawns to autumn that varied inversely with adult (2+) female density. In contrast to Gavin et al. (1984), comparatively low fawn survival at high female density resulted from social interaction between females rather than from a deteriorating influence of deer on their habitat. Social interaction may have been a predisposing factor in summer fawn mortality. A similar hypothesis resulted from experimentation on an enclosed population of white-tailed deer maintained on a high nutritional plane (Ozoga et al. 1982, Ozoga and Verme 1982). However, they did not relate observed phenomena to physical and biological characteristics of the habitat.

The matriarchal social organization of white-tailed deer (Hawkins and Klimstra 1970, Hirth 1977) was apparent from the comparatively small movement indexes and comparatively high home range stability among mature females during summer. Ozoga et al. (1982) hypothesized that parturition territoriality enhances reproductive success of matriarchal does presumably at the expense of younger socially-subordinate parous does. Ozoga and Verme (1982) also attributed density dependent mortality of fawns during summer to failure of proper imprinting and/or abandonment by socially subordinate females. Reproductive success on the lower Yellowstone varied inversely with abundance of adult (2+) females regardless of age, though changes in density apparently had greater influence on fawn rearing success among 2- and 3-year old females. Ozoga et al. (1982) and Ozoga and Verme (1982) indicated only younger females were affected, whereas our data indicated that ability of prime age and older females to successfully rear fawns was also affected at high density.

It is highly probable that 2- and 3-year old females, by virtue of their subordinate social status, may experience comparatively more difficulty rearing fawns than older females (Ozoga and Verme 1986). This may have contributed to reproductive failure in successive years among some younger females, a phenomenon not observed among prime aged (4-7 yrs.) females.

We have no evidence to suggest that predation directly limited population growth or that its role varied with population density. Studies in Texas (Cook et al. 1971, Beasom 1974, Carroll and Brown 1977) singled out density-related predation on newborn fawns as a factor that may stabilize or limit population size in the semiarid southwestern region of the U.S. More

favorable cover conditions at bedding sites contributed to somewhat lower fawn mortality in the agricultural Midwest, though predation was also a factor (Huegel et al. 1985). In New York, a rate of fawn mortality, similar to that in the Midwest, was reported by O'Pezio (1978) that was not influenced by predation or human interference.

We also have no evidence to indicate that density dependence manifested itself in adult mortality or an endocrine feedback between social behavior and population size as hypothesized by Christian and Davis (1964). Experimentation with a confined herd of white-tailed deer provided with excellent nutrition indicated no density-dependent response in adrenal weight or secretory activity up to densities of 63 deer/ km^2 (Seal et al. 1983) that exceeded densities observed during this study.

Our data suggest that feedback between social behavior and population size was related to allocation of forage/cover resources during summer as reflected in reproductive potential and recruitment. Such a strategy favors minimal fawn recruitment at habitat "fill" and a "compensatory" response in recruitment following a reduction in female density by either natural or artificial means as reported by Swenson (1985) for mountain goats (Oreamnos americanus). Habitat fill is defined as the relative numbers or density of deer a habitat may sustain over time and space including all biological and physical attributes of a given habitat that influence deer numbers (Mackie 1983).

The absence of behavioral spacing of females during summer could result in less than optimal recruitment of fawns to autumn. Adams (1960) speculated that a breakdown in spatial separation, attributable to overcrowding and subsequent displacement of deer into marginal habitats, may be a density dependent factor limiting population growth. At low density, all females on the lower Yellowstone, despite behavioral spacing, were able to occupy optimal habitats, and fawn recruitment to autumn was high. At medium densities, many young adult females occupied marginal habitats, and thus, lost one or both fawns. At high densities, not only did the rate of fawn recruitment decline among young adult females, but increased social interaction resulting from greater mobility of these younger females probably inhibited reproductive success of prime-age and old females.

The role of maternal investment in female offspring through the first 3 years of life in maintaining population stability was consistent with hypotheses of Gavin et al. (1984) and Clutton-Brock et al. (1983) in its implication that regulation occurs at the level of the matrilineal group. The selection process perhaps favored females that successfully occupied small home ranges in vegetatively and structurally diverse habitats. Consequently, they reared more female fawns as a function of total fawn survival. Subsequent generations of females in those matrilineal groups, with increasing age and experience, also used those sites. Exceptions were those females making extensive home range shifts as yearlings or as 2 year-olds that included

dispersal from the river bottom environment. Tolerance for subadult female offspring around the periphery of their territory by female black bears (Ursus americanus) was offered by Rogers (1987) as an explanation for a comparatively lower rate of dispersal among young females than among males. Female philopatry may also explain an apparent decline in summer home range size among mature female white-tailed deer from medium to high female density.

Influence of Dispersal.--Although yearling males were more prone to disperse from ancestral home ranges than females, the low rate of dispersal of individuals from the river bottom study area did not measurably influence population size or the sex ratio of yearlings. Over 80% of yearling dispersals on the lower Yellowstone were confined to the river bottom despite higher deer densities than on surrounding uplands. This occurred during a period in which the river bottom population nearly doubled in size. Egress and ingress of yearling deer was documented in each of the intensive study areas suggesting that dispersal had a minimal effect on population dynamics among subpopulations.

Sexual competition between males, prior to and during the breeding season, has been considered a major factor influencing the comparatively high rate of dispersal among yearling males (Downing and McGinnes 1975, Kammermeyer and Marchington 1976, Bunnell and Harestad 1983). The lower affinity of yearling males than females to their matriarchal groups (Hawkins and Klimstra 1970) may explain differential rates of dispersal between yearling males and females. However, Ozoga and Verme (1985) reported that dominant yearling males were less inclined to remain in ancestral home ranges than their subordinate cohorts at the onset of breeding; this behavior was observed even in the absence of older males. They also reported the most intense social interaction between yearling males and related older females occurred prior to and during the breeding season when we observed comparatively high rates of dispersal of yearling males. Most dispersal of yearling females occurred during May-August when social interaction with older females was probably most intense. Thus, dispersal of both sexes of yearlings from ancestral home ranges may have resulted from social interaction with adult females within family groups.

Dispersal of yearling males may optimize inbreeding from its capacity to faithfully transmit adaptive parental gene combinations (Nelson and Mech 1984). Perhaps of greater consequence, is the role of proportionately high male dispersal, along with greater parental investment in female offspring, or female philopatry, in allowing optimal resource partitioning in polygamous species as implied by Rogers (1987). This may reflect a more plausible implication of dispersal to a strategy of social population regulation than one involving a direct reduction in population size through dispersal as proposed by Hawkins et al. (1971).

Influence of Other Factors.--Catastrophic mortality among adult whitetails during late summer and early autumn that strongly implicated EHD as the causative agent was not density-related. The outbreak in eastern Montana in 1977 was most significant on the lower Yellowstone River, claiming approximately one-third of the population in the Intake area (Swenson 1979). This presumably contributed to the population decline in the late 1970s.

The EHD virus was first isolated in eastern Montana following a 1978 outbreak and was identified as serotype 2 implying that cattle and mule deer may be passively involved in transmission of the virus (Feldner and Smith 1981). Their data confirmed that high mortality was limited to white-tailed deer. Other outbreaks of hemorrhagic disease occurred in eastern Montana in 1961, 1976, 1977, and 1978 with a few scattered reports of dead deer in 1970 and 1971 (Walcheck 1978). A major epizootic was reported for southwestern North Dakota in 1970 and a lesser one for 1971 (Hoff et al. 1973). All occurred from late July through October. Other diseases affecting white-tailed deer are of little consequence in the Great Plains region (Petersen 1984).

Influence of Hunting.-- Hunting was the single largest mortality factor during all years. A time lag model (McCullough 1979) indicated that the annual rate of population change and population size were in equilibrium from 1980 to 1983 when the population was increasing (Fig. 18). As pre-hunt populations increased from 1980 to 1983, proportionately larger segments of the population were removed by hunting (Table 18), with some possible time-lag delay coinciding with liberalized hunting seasons from 1983 through 1985. Adult mortality, attributable to causes other than hunting, was generally very low regardless of population size.

A sex ratio among yearling and older deer favoring females at a rate of approximately 2:1 appeared solely attributable to hunting. Our data suggested that hunters selected antlered over antlerless deer (Tables 19 and 20), although numbers of antlered deer taken by hunters varied directly with their abundance in the population. The relatively young age structure of males also reflected disproportionately greater removal of males by hunting, because mortality from other factors, except highway mortality during December-May, did not suggest any differential mortality. However, in the absence of hunting, natural mortality among adults may also claim disproportionately more males than females as reported for the lower Columbia River where adult females outnumbered males by a ratio of approximately 3:1 (Gavin et al. 1984).

Among yearlings, disproportionately higher dispersal of males than females might suggest that males were more vulnerable to hunting by virtue of occupying unfamiliar habitat. The coincidence of a decline in the relative proportion of yearling males in annual harvests and declining antler growth suggested

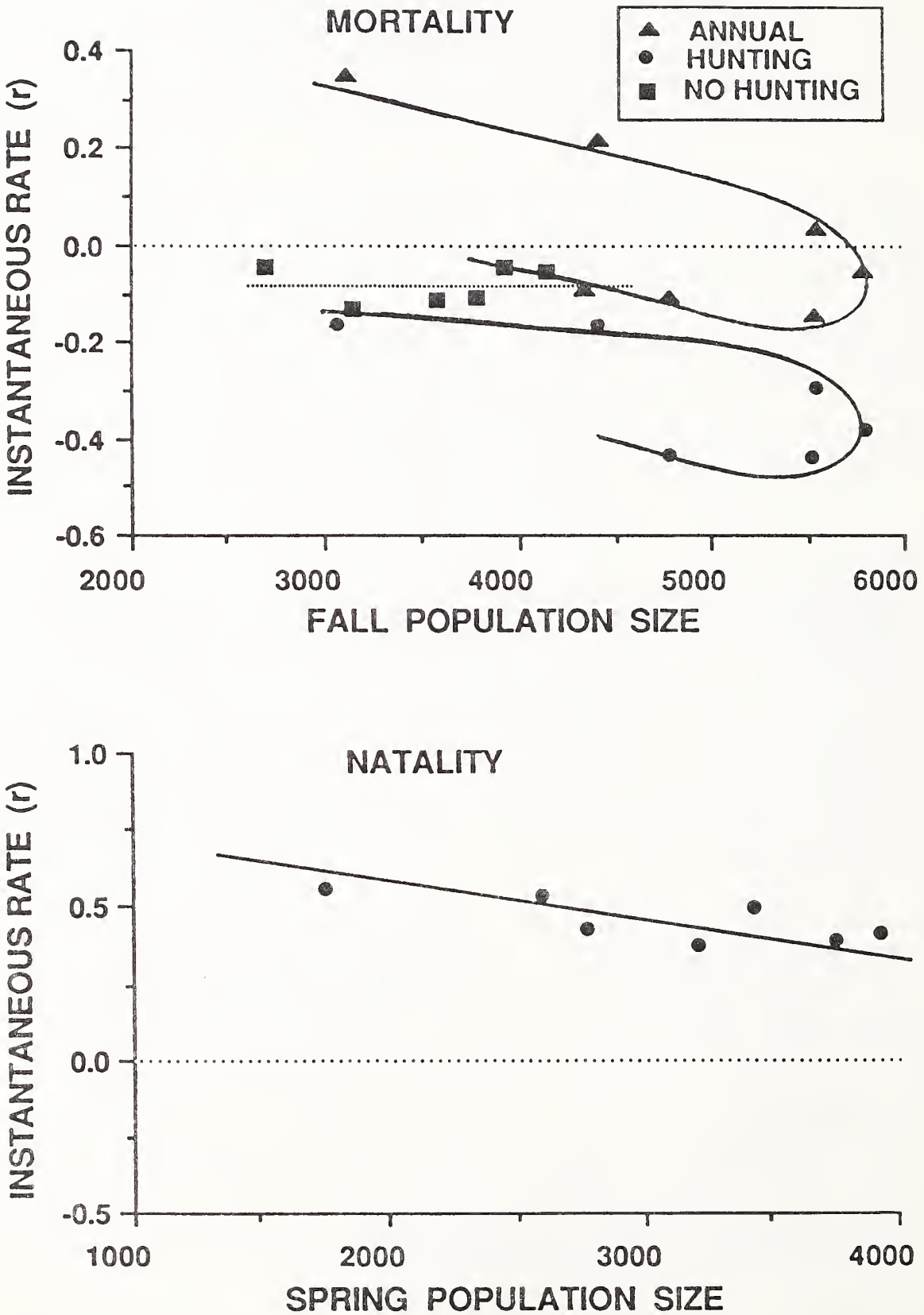


Figure 18. Time lag model of rate of change versus population size considering the effects of mortality and natality.

that disproportionate higher mortality was an artifact of hunter selectivity for antlered deer and probably larger over smaller antlers. Selectivity also appeared dependent upon hunters differentiating yearling males from antlerless deer.

The increased antlerless harvest from 1982 to 1985 (Table 19) reflected liberalized bag limits for antlerless deer that included multiple tags per hunter in 1984 and 1985. Hunters tended to take adult females over fawns during 1980-83. A greater proportion of fawns in annual harvests in 1984 and 1985 probably reflected less hunter-selectivity between fawns and adult females when more than one antlerless deer could be taken per individual hunter.

The effect of exploitation of antlerless deer was the overridding factor influencing population size and trend from 1983 through 1985 when harvest rates equalled or exceeded recruitment rates (Tables 5 and 18). The river bottom population declined from 1983 to 1986 despite a compensatory increase in fawn survival in response to declining female density (Fig. 7).

Comparatively greater stability among numbers of adults and higher, more stable recruitment rates at Elk Island than at Intake (Tables 4 and 6) may have reflected the relative influence of hunting in the respective areas. Because of greater hunter access during all years, continuous harvesting of antlerless deer at Elk Island resulted in lowered female density that was compensated by higher recuitment of fawns than observed at Intake. Average yearly gains through recruitment of fawns to autumn, expressed as a percent of total numbers of yearling and older deer during summer, were 60% (49-67%) at Elk Island and 53% (39-67%) at Intake. Because of relatively little exploitation from 1980 through 1983 at Intake, numbers of adults increased and recruitment sharply dropped off (Table 4).

Gavin et al. (1984) and Woolf and Harder (1979) attributed disproportionately high natural mortality among adult males to stress associated with breeding activity. Our data suggest that hunting mortality among males compensated for natural mortality, because males older than 4 years, that would be predisposed to natural mortality from the cumulative energetic cost of breeding, accounted for less than 1% of all males.

From a hypothetical 1,000 yearling males in a pre-hunt population, and assuming an average annual mortality rate of 60% for yearling and older males determined from annual population estimates (Table 16), only 26 (3%) can be expected to live to an age of 5 years. Thus, few males reach an age where they might be predisposed to overwinter mortality from energy-related stress of breeding behavior. Similarly for females, 370 (37%) of 1,000 yearlings can be expected to live to an age of 5 years, and 175 (18%) can be expected to reach an age of 8 years. The average annual mortality rate of yearling and older females for all years was 22% (Table 16). The minimum age where females were predisposed to overwinter mortality appeared to be 8-9 years,

whereas the only documented case among individually marked adult males was a 4-year-old.

During 1983-85, when harvest of antlerless deer was highest (Table 19), average annual mortality of all adult (1+) females from all causes was 34%. From a hypothetical 1,000 yearling females, 190 could be expected to reach an age of 5 years if that mortality rate were constant over time; 50 could be expected to reach an age of 8 years. Continuous annual turnover of one-third or more of the females would result in a much younger age class structure. Hunting mortality appeared to offer less opportunity for compensatory mortality among females than among males.

Because female mortality from causes other than hunting was minimal, natural regulation of female numbers would be achieved through density-dependent rates of recruitment and attrition of females older than 8 years.

MANAGEMENT IMPLICATIONS

Both population density and habitat use during our study were indicative of the manner in which deer encountered, exploited, and responded to varying habitat characteristics. Major habitat components, vegetation, topography, land use, and climate, interacted with behavioral attributes of the deer to influence distribution, movements, use of specific habitats, and food habits.

In part, our findings departed from traditional models of population regulation for white-tailed deer. However, they attest to the wide ecological amplitude previously documented for the species. Each environment occupied involves an adaptive strategy by which the particular population may successfully exploit its particular habitat and persist over time. These in turn are reflected in different population characteristics and dynamics between habitats. Management of white-tailed deer in riverine environments in the northern Great Plains should consider:

1. White-tailed deer on the lower Yellowstone River were closely associated with mid to late seral communities of the grassland sere. Relative density of deer varied directly with abundance of riparian forest and shrub cover: a strong linear relationship suggested a continuum of density distribution of deer with that of riparian cover. Limited water management and land use practices on the lower Yellowstone, that includes minimal competitive partitioning of the riparian habitat by ungulates, have probably contributed to a relatively stable habitat favoring comparatively high densities of white-tailed deer. Under more intensive water management that pre-empts periodic flooding, including channelization or mainstem impoundment, the regional climax vegetation (grassland) would ultimately become more prevalent at the expense of mid to late seral

communities (Boggs 1984). Any significant alteration of river flow and dynamics that resulted in a reduction of riparian tree/shrub cover would ultimately result in a reduction of base densities of white-tailed deer.

2. Land clearing for field development, or logging, that reduced the amount of mature stands of cottonwood with a tree/shrub understory on the floodplain may reduce deer numbers locally. However, clearing small stands of decadent cottonwood that contained a grass understory and planting them to legume or cereal crops may benefit deer by creating additional diversity and interspersion of the 2 important habitat components. If employed on wildlife management areas, this may also provide an attractive alternative to other means of abating depredation by deer on agricultural crops.

3. Seasonal shifts in distribution reflected a preference during summer, at least among adult females, for diverse habitats, or the amount of edge, created by the interspersion of riparian communities and irrigated agricultural fields. During winter, all deer used relatively large blocks of riparian cover during daytime periods, while moving up to 1-2 km at night to feed in agricultural fields. Agricultural crops provided deer with readily digestible, high energy forage yearlong. A temporal dichotomy in relative use of crops by adult males and females reflected a period of high energy demand in the respective sexes: following the breeding season among males and during late gestation and lactation among females. The presence of this source of forage enhanced productivity and minimized natural mortality of deer older than 4 months, thus pre-empting a relationship between population dynamics and density with condition and trend of key browse species. Whereas the abundance of riparian tree/shrub cover may be overriding in its influence on the overall density distribution of deer on the river bottom, crop type and availability of crop residues influence which fields are used.

4. The traditional "limiting" role of winter forage was not applicable to white-tailed deer on the lower Yellowstone River. Such a consideration perhaps may be extended to white-tailed deer in other riverine habitats in the northern Great Plains where climatic variability is buffered by irrigated agriculture. In riverine environments, natural population regulation may be achieved through allocation of forage and cover resources by social spacing among adult females. Variability in reproductive potential with changes in population size and/or environmental variability may reflect relegation of socially subordinate females to less than optimal summer habitats.

5. Exploitation of the population by hunting was an overriding factor contributing to a decline in population numbers from 1983 through 1986. The decline occurred despite a compensatory increase in fawn survival over summer in response to reduced female density because hunting-related mortality equalled or exceeded recruitment. Our data indicated that other factors contributing to mortality of adult females were additive to that of hunting and did not change in response to changes in animal abundance. Population declines, precipitated by heavy exploitation of antlerless deer, were not limited to periods of comparatively low fawn recruitment as generally implied from the trend for the entire river bottom study area or at Intake specifically. A population decline also occurred in the Elk Island subpopulation from 1984 to 1985 despite an increase in recruitment from 76 to 106 fawns:100 adult females between the 2 years. This type of compensatory increase in recruitment may be limited to riverine habitats where availability of irrigated agricultural crops to deer buffer the effects of variable climatic conditions on availability of natural forage.

6. The level of exploitation of antlered deer by sport hunting (58%) during our study that resulted in a relatively young age class structure among males had no apparent effect on population dynamics or trend. However, removal of 30-33% of the females older than fawns by hunting resulted in population declines; continuous harvesting at these levels would result in a younger age class structure than existed during this study. Removal of 26% of yearling and older females roughly maintained female numbers at the same level between years, and harvests of less than 20% were followed by population increases. Therefore, removal of 20-25% of those age classes of females should be sustainable in this habitat, though special antlerless whitetail regulations were necessary to achieve that level of harvest during this study.

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